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Functional Craniology of the Ceratopsia
(Reptilia: Ornithischia)
with Special Reference to *Eoceratops*

by

© H. TYSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Functional Craniology of the Ceratopsia (Reptilia: Ornithischia) with Special Reference to Eoceratops submitted by Helen Tyson in partial fulfilment of the requirements for the degree of Master of Science.

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Date 17 October 1977

ABSTRACT

The specimen upon which much of the present study is based, UA 40, was tentatively assigned to Eoceratops by Gilmore, in 1923. Gilmore was unable to make a positive assignment because at that time, UA 40 was still largely imbedded in rock matrix. Further, the only other specimen of Eoceratops (NMC 1254, upon which the type species, E. canadensis, is based) is incomplete; so much so, in fact, that Ostrom (1966) considered the genus indeterminate. In the course of the present study, however, UA 40 was prepared more completely and is now assigned without question to Eoceratops, removing any possibility of that genus being indeterminate.

In attempting to determine the affinities of Eoceratops, several lines of approach were used: comparison of osteologic features, reconstruction of cranial muscles, study of the mandibular mechanics and study of the properties of the skull related to resisting and transmitting imposed stresses. From the results of these inquiries, it became apparent that Eoceratops is most closely related to Chasmosaurus, although it appears to be a side branch off the main Chasmosaurus lineage. Arrhinoceratops and Triceratops also are related to Eoceratops and these, and related genera, belong to a larger, "long-squamosaled" lineage. Monoclonius,

Centrosaurus, *Styracosaurus*, *Brachyceratops* and *Pachyrhinosaurus*, on the other hand, form a separate lineage of "short-squamosaled" ceratopsians with very different adaptations.

ACKNOWLEDGEMENTS

Many people contributed their time and resources to this study. Dr. D. A. Russell, of the National Museums of Canada, Paleontology Division, very kindly lent the type material of Eoceratops canadensis, as well as providing enlarged photographs of Leptoceratops from an article published by C. M. Sternberg in 1951. Mr. P. Currie, of the Alberta Provincial Museum and Archives, also loaned specimens for study.

Dr. R. C. Fox, of the University of Alberta, Dr. E. Gaffney, of the American Museum of Natural History, Dr. J. H. Ostrom, of the Yale Peabody Museum, and Dr. D. A. Russell allowed me to view the specimens under their care and went to considerable effort to remove cases from specimens on display for this purpose. In addition, I am indebted to Drs. Ostrom and D. Baird, of Princeton University, for allowing me to examine and publish drawings of the isolated Leptoceratops teeth (PU 18133) shown in Fig. 30, to Dr. J. E. Storer for helpful discussions concerning ceratopsians and available ceratopsian material, and to Dr. Fox, Mr. H.-D. Sues and Mr. B. G. Naylor for stimulating discussions on topics related to this thesis.

Mr. Naylor lent specimens of isolated hadrosaur and ceratopsian teeth. Mr. A. Lindoe provided invaluable advice concerning the preparation and photographing of specimens

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and Mr. R. G. Tyson did the lettering for all the illustrations in this text.

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UA 40, the specimen of Eoceratops canadensis upon which much of this study was based, was collected by G. F. Sternberg, in 1920.

TABLE OF CONTENTS

Abstract iv

Acknowledgements vi

Table of Contents viii

List of Figures x

Table of Abbreviations xvii

Introduction 1

CHAPTER PAGE

I. Description of Eoceratops 3

(a) Description of type material 3

(b) Description of UA 40; comparison with NMC 1254 ...40

(c) Revised description of the genus Eoceratops 66

II. Functional Craniology 69

(a) Reconstruction of the musculature 69

(b) Dentition 174

(c) Mandibular mechanics 204

(d) Stress transmission in ceratopsian skulls 241

(e) Structure and function of the frill 292

III. Phylogeny of the Ceratopsia 309

TABLE OF CONTENTS continued

(a) Relationships of Eoceratops 309

(b) Trends in structure within the

Ceratopsia 315

Summary 318

Literature Cited 321

LIST OF FIGURES

Figure Page

1. Right squamosal (NMC 1254a) of type specimen of *Eoceratops canadensis*, x.20. a. Lateral view. b. Medial view. 10

2. Right squamosal (NMC 1254a) and anterior extension of right parietal (NMC 1254b) of type specimen of *Eoceratops canadensis*, x.20. 16

3. Right postorbital, frontal and prefrontal (NMC 1254d) of type specimen of *Eoceratops canadensis*, x.20. a. Lateral view. b. Ventro-medial view. 21

4. Right nasal (NMC 1254c) of type specimen of *Eoceratops canadensis*, x.25. a. Lateral view. b. Medial view. 29

5. ?Postcranial fragment (NMC 1254) of type specimen of *Eoceratops canadensis*, x.45. a. "Dorsal" view. b.

LIST OF FIGURES continued

"Ventral" view. 34

6. Left dentary (NMC 1254e) of type specimen of *Eoceratops canadensis*, x.30. a. Lateral view. b. Medial view. 36

7. Anterior dorsal or posterior cervical vertebra (NMC 1254) of type specimen of *Eoceratops canadensis*, x.35. a. Anterior view. b. Posterior view. 38

8a. Skull of UA 40 (*Eoceratops canadensis*), left lateral view, x.22 (photograph). 42

b. As for a (drawing). 44

9. Right squamosal (NMC 1254a) (image reversed) of type specimen of *Eoceratops canadensis*, superimposed on the left squamosal of UA 40 (*E. canadensis*), x.29. 47

10. Right postorbital, frontal and prefrontal (NMC 1254d) (image reversed) of type specimen of *Eoceratops canadensis*, superimposed on the left postorbital, frontal and prefrontal of UA 40 (*E. canadensis*), x.27. 50

11. Right nasal (NMC 1254c) (image reversed) of type specimen of *Eoceratops canadensis*, superimposed on

LIST OF FIGURES continued

the left nasal of UA 40 (*E. canadensis*), x.27. 54

12. Medial surface of the jugal of UA 11735 (*Centrosaurus* sp.). 86

13. Left supratemporal fossa of UA 11735 (*Centrosaurus* sp.) and left lateral view of the same skull. 97

14a. Lateral view of anterior, hook-shaped process on coronoid process of right dentary of ROM 4519 (*Centrosaurus apertus*). b. Medial view of right dentary of UA 41 (*Centrosaurus* sp.). 116

15. Lateral view of left epipterygoid of a. AMNH 6325 (*Pentaceratops sternberghii*) and b. AMNH 5239 (*Centrosaurus flexus*). 121

16. Lateral view of right ramus of lower jaw of ROM 4519 (*Centrosaurus apertus*). 123

17. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored with superficial musculature, x.20. 136

18. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored with musculature, x.20. 138

LIST OF FIGURES continued

19. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored with deep musculature, x.20. 140

20. Dorsal view of supratemporal fossae of a. NMC 344 (*Styracosaurus albertensis*), x.06 (from Lull 1933); b. AMNH 5402 (*Chasmosaurus belli*), x.07 (from Lull 1933); and c. YPM 1823 (*Triceratops serratus*), x.08 (from Hatcher, Marsh and Lull 1907). 145

21. Dorsal view of skull of NMC 8889 (*Leptoceratops gracilis*), muscles and fascia partially restored, x.43. (Drawn from a photograph originally published by Sternberg (1951). Through the courtesy of Dr. D. A. Russell and the National Museums of Canada.) 152

22. Areas of muscle attachment on the occiput and ventral frill surface of UA 11735 (*Centrosaurus* sp.). 165

23. Areas of muscle attachment on the occiput of NMC 2280 (*Chasmosaurus belli*). 168

24. Areas of muscle attachment on the occiput of AMNH 6254 (*Psittacosaurus mongoliensis*). 172

LIST OF FIGURES continued

25. Left lateral view of preserved portions of maxillary dentition of UA 40 (*Eoceratops canadensis*), x1. 176

26. Functional series of isolated teeth illustrating the rotation of the occlusal plane in ceratopsids with respect to the base of the crown. a. and e., APM P67.8.5, x1.56 and 1.51, respectively; b. and f., APM P66.33.4, both x1.43; c. and g., APM P67.18.1, both x1.61; and d. and h., APM P64.5.199, x1.58 and 1.40, respectively. 182

27. Occlusal view of isolated ceratopsid tooth (APM P64.5.199), x7. 187

28. Medial view of right dentary of UA 41 (*Centrosaurus* sp.). 190

29a. ?Anterior view of single vertical series from the dentary of *Anatosaurus anectens* (from Lull and Wright 1940), x1.08. b. Lingual view of dentary teeth of unidentified hadrosaur (UA 11734), x3.4. 192

30. Isolated *Leptoceratops* tooth (PU 18133) from dentary, x2.88. a. and c., ?anterior view; b. and d., occlusal view. (Through the courtesy of Drs. J. H. Ostrom and D. Baird and Princeton

LIST OF FIGURES continued

University.) 201

31. Right lateral view of rostral and premaxillary flange of a. YPM 1821 (*Triceratops flabellatus*) and b. AMNH 1624 (*Pentaceratops* sp.). 207

32a. Right lateral view of rostral and premaxillary flange of ROM 4519 (*Centrosaurus apertus*). b. Left lateral view of premaxillary flange of ROM 5135 (*Arrhinoceratops brachyops*). 210

33. Various methods for increasing the moment arm of the major jaw adductors of ceratopsians. 222

34. Left lateral view of the skull of a. *Centrosaurus* and b. *Leptoceratops*. 226

35. Oblique occlusal view of dentary teeth of unidentified hadrosaur (UA 11734), x4. 233

36. Functional series of isolated teeth (UA 207) illustrating the lack of rotation of the occlusal plane in hadrosaurs. a. and d., x2.56; b. and e., x2.56; and c. and f., x2.75. 236

37. Left lateral view of the skull of AMNH 5240 (*Corythosaurus casuarius*) (from Ostrom 1961). 238

LIST OF FIGURES continued

38a. Left lateral view of skull of UA 11735 (Centrosaurus sp.). b. Detail of left squamosal of UA 11735. c. Anterolateral view of right antorbital region of YPM 1830 (Torosaurus latus). 306

TABLE OF ABBREVIATIONS

BONES

An - Angular

Ar - Articular

Bo - Basioccipital

CV - Fused anterior cervical vertebrae (I, II and III)

D - Dentary

Ec - Ectopterygoid

Ej - Epijugal

En - Epinasal

Ex - Exoccipital

FM - Foramen magnum

J - Jugal

L - Lacrimal

Mx - Maxillary

N - Nasal

OC - Occipital condyle

P - Parietal

Pf - Prefrontal

Pm - Premaxillary

Po - Postorbital

Pt - Pterygoid

TABLE OF ABBREVIATIONS continued

Q - Quadrate

Qj - Quadratojugal

Sa - Surangular

Sq - Squamosal

MUSCLES and LIGAMENTS

l.n. - *ligamentum nuchae*

M.a.-p. - *M. articulo-parietalis*

M.a.m.e.m. - *M. adductor mandibulae externus medialis*

M.a.m.e.p. - *M. adductor mandibulae externus posterior*

M.a.m.e.s. - *M. adductor mandibulae externus superior*

M.d.m. - *M. depressor mandibulae*

M.il.-c.cap. - *M. ilio-costalis capitis*

M.il.-c.cer. - *M. ilio-costalis cervicis*

M.im. - *M. intermandibularis*

M.l.a.o. - *M. levator anguli oris*

M.l.b. - *M. levator bulbi*

M.o.c.m. - *M. obliquus capitis magnus*

M.pst. - *M. pseudotemporalis*

M.pt.-m. - *M. pterygo-mandibularis*

M.r.c.p. - *M. rectus capitis posterior*

?M.scm. - ?*M. sternocleidomastoideus*

M.sp.cap. - *M. spinalis capitis*

M.sv. - *M. subvertebralis*

M.tr.cap. - *M. transversalis capitis*

TABLE OF ABBREVIATIONS continued

M.tr.cer. - *M. transversalis cervicis*

?s.a. - possible anterior slip of *M*.*a*.*m*.*e*.*s*.

INSTITUTIONS

AMNH - American Museum of Natural History

APM - Alberta Provincial Museum and Archives

NMC - National Museums of Canada

PU - Princeton University

ROM - Royal Ontario Museum

SMVP - St. Paul Science Museum

UA - University of Alberta

USNM - U. S. National Museum

YPM - Yale Peabody Museum

Functional Craniology of the Ceratopsia
(Reptilia: Ornithischia)
with Special Reference to *Eoceratops*

Introduction

In 1902, Lambe described a new ceratopsian, *Monoclonius canadensis*, based on a well preserved but fragmentary specimen. Subsequently, owing to the incomplete nature of the type specimen, *M. canadensis* received a variety of taxonomic designations from other workers before Lambe (1915) re-assigned it to a new genus, *Eoceratops*. After this final designation, the specimen received little attention and Ostrom (1966) went so far as to label *Eoceratops* indeterminate. In 1923, Gilmore assigned a second specimen to *Eoceratops* but the specimen was only partially prepared, so the assignment was provisional and did little to affect the uncertain status of the genus. (Lull (1933), in fact, did not believe that this specimen belonged to *Eoceratops* at all (see below).) Recently, this second specimen (UA 40) has been prepared completely on one side with the braincase, supratemporal fossae, palate and occiput being exposed, as well. In all comparable parts, UA 40 is sufficiently similar to the type specimen of *Eoceratops canadensis* to be included in the same taxon so that the genus *Eoceratops* now is known in enough detail to eliminate any possibility of it being indeterminate.

In the course of analysing the various cranial features of Eoceratops, it became evident that the genus occupied an important position in the phylogeny of the Ceratopsidae and in order to elucidate that position, it became necessary to expand the study to include as many members of the Suborder Ceratopsia as possible. This work is not in any sense a taxonomic revision, but rather a survey of certain structural characteristics and their possible functions. Since fairly complete specimens are required to make meaningful inferences in functional anatomy, many of the specimens that would be considered in a taxonomic revision are ignored here but all valid genera are covered, with varying degrees of thoroughness, and the results are used to construct a possible phylogeny for the Ceratopsidae. It is hoped that this study will be of use not only in providing a more complete description of the genus Eoceratops but in describing and attempting to explain the functions of various features of ceratopsian cranial anatomy.

I. Description of *Eoceratops*

(a) Description of type material

In his original description, Lambe (1902) founded the species *Monoclonius canadensis* on disarticulated cranial elements and an anterior dorsal vertebra from one individual, the right dentary of another individual, a separate ?nasal horn core, a separate tooth and a right maxillary (with teeth).

The bulk of the material, belonging to a single individual (NMC 1254), was discovered by Lambe, in 1901, "on the east side of the Red Deer river, Alberta, a short distance below the mouth of Berry creek" (Lambe 1915, p.1). The right dentary (NMC 284) was found separately in 1897 (Lambe 1902). Lambe (1902) included this element in the type material of *Monoclonius canadensis* because it is similar in size to the left dentary of NMC 1254 but the dentaries of ceratopsids show too little variation to be the sole means of generic or specific identification. Therefore, since NMC 284 was not found in the same locality as the rest of the type material, it must be considered indeterminate.

The separate ?nasal horn core is utterly unlike that of NMC 1254 but since Lambe (1902) originally identified the nasal of NMC 1254 as the jugal, he was unaware of the discrepancy at the time he assigned this specimen to *Monoclonius canadensis*. Probably, the horn core belongs to

Centrosaurus, for it has many of the characteristics of the nasal horn core of that genus (Sternberg 1938), but it cannot be included in the type material of Monoclonius canadensis.

In his 1902 paper, Lambe did not figure the right maxillary (NMC 285) that he referred to Monoclonius canadensis, although he figured one tooth from this element (Lambe 1902, pl. XVIII, figs. 3 and 4) and he used NMC 285 for his (1915) restoration of Eoceratops canadensis. In describing this maxillary, Lambe (1902, p.66) stated only that the "teeth are double fanged" and gave no further information regarding this specimen, which was found on the west side of the Red Deer River. Since isolated ceratopsid maxillaries are insufficient evidence for generic determination, and since this specimen was found separately from the major portion of the type material (NMC 1254), NMC 285 also must be considered indeterminate.

Lambe (1902) referred the separate (dentary) tooth to Monoclonius canadensis on the basis of its double-rooted structure but all ceratopsids have double-rooted teeth (even Lambe (1902, p.65) admitted that several species share this characteristic), so this tooth cannot be assigned to any particular genus within the Ceratopsidae.

Thus, all of the material referred by Lambe (1902) to Monoclonius canadensis is indeterminate, except those portions belonging to the single individual NMC 1254. Although no one has stated directly that the rest of this material is indeterminate, there appears to be a consensus on this point, as both Hatcher, Marsh and Lull (1907) and Lull (1933) listed only the material belonging to NMC 1254.

Hatcher (Stanton and Hatcher 1905) referred NMC 1254 to the genus "*Ceratops*", saying later (Hatcher, Marsh and Lull 1907, p.95) that

> "the discovery of this specimen is of the greatest importance, since it affords the first definite information regarding the character of the parietals and squamosals that are associated with the type of frontal horn cores shown in Marsh's type of *Ceratops montanus*. A comparison of the frontal horn of the type of the present species ["*Monoclonius*" *canadensis*] with that of Marsh's type of *C. montanus* makes it apparent that they are essentially the same, and I do not hesitate to remove the present species from the genus *Monoclonius* Cope and place it in that of *Ceratops* Marsh. Whether or not it should be regarded as specifically distinct from *C. montanus* I am unable to say without further study".

Hatcher did not live to complete the revision of genera and species in which he intended to settle this question and that portion of the monograph was undertaken by Lull. Of the differences between *Ceratops montanus* and NMC 1254 Lull (Hatcher, Marsh and Lull 1907, p.172) said: "the only distinction must lie in the character of the supraorbital horn cores, which, although Hatcher considers them 'essentially the same,' seem to differ in that the base is subtriangular in section in *C. montanus* and circular in *C. canadensis*." Noting further that the curvature of the brow horn cores is different in these two species, Lull (Hatcher, Marsh and Lull 1907) left NMC 1254 in *Ceratops canadensis*.

By 1915, Lambe had changed his own ideas concerning this specimen, since by then he felt that both *Monoclonius* and *Ceratops* were invalid taxa. Lambe (1915, p.11) noted that the assignment to the genus *Ceratops* of specimens other than the type material of *C. montanus* had led Hatcher (Stanton and Hatcher 1905; Hatcher, Marsh and Lull 1907) "to assign characters to Ceratops [*sic*] for which there was no warrant in the generic type." The genus *Ceratops* was founded by Marsh, in 1888, on the brow horn cores and occipital condyle of a single individual from the Judith River beds on Cow Creek, Montana (Lull 1933). (The name "*Ceratops*" was given to a genus of birds by Rafinesque in 1815 (Lull 1906) but since "no description of the genus was published, and as no forms were mentioned as pertaining to it, it becomes a nomen nudum [*sic*]" (Hatcher, Marsh and Lull 1907, p.100).) The type material of *Ceratops montanus* is too fragmentary to be assigned to a genus or species within the Ceratopsidae and the other specimens assigned to *Ceratops* (Stanton and Hatcher 1905) all have been removed to other taxa. "*Ceratops*" *paucidens* was referred to a hadrosaur, *Lambeosaurus*, by Ostrom (1964*c*); Lull (1933) placed "*C.*" *recurvicornus* in *Monoclonius*, its original assignment before Hatcher (Stanton and Hatcher 1905) placed it in *Ceratops*, but Sternberg (1938) considered it to be a species of *Centrosaurus*; "*C.*" *belli* is now *Chasmosaurus belli* (Lambe

1914b;[1] and "C." canadensis is now Eoceratops canadensis (Lambe 1915). Since the type specimen of Ceratops montanus is too fragmentary to allow meaningful comparisons with other specimens, no further material can be referred to either the genus Ceratops or the species C. montanus. The indeterminate state of the genus Ceratops does not affect the validity of the name Ceratopsidae, however, so it is not necessary to adopt Cope's "Agathaumidae", as Lull had suggested in 1906.

Lambe (1915, p.12) felt that the genus Monoclonius also was "in a very unsatisfactory state" and was "not sufficiently defined for use" (1915, p.14), so he removed the type material of M. canadensis to Eoceratops canadensis.[2] As mentioned above, of all this material, only that pertaining to a single individual (NMC 1254) can be retained in Eoceratops canadensis; the rest, being indeterminate, is not considered in this study.

Although fragmentary, the type material of Eoceratops canadensis is well preserved. The largest element is the right squamosal (NMC 1254a), which is essentially complete, missing only small parts of the posterior and anterior edges (Fig. 1a, b). As in *Triceratops* (Lambe 1915; Lull 1933), the squamosal is roughly triangular in outline and as in *Centrosaurus* and *Styracosaurus*, it is relatively short, although in *Centrosaurus* and *Styracosaurus* the squamosal is rectangular.

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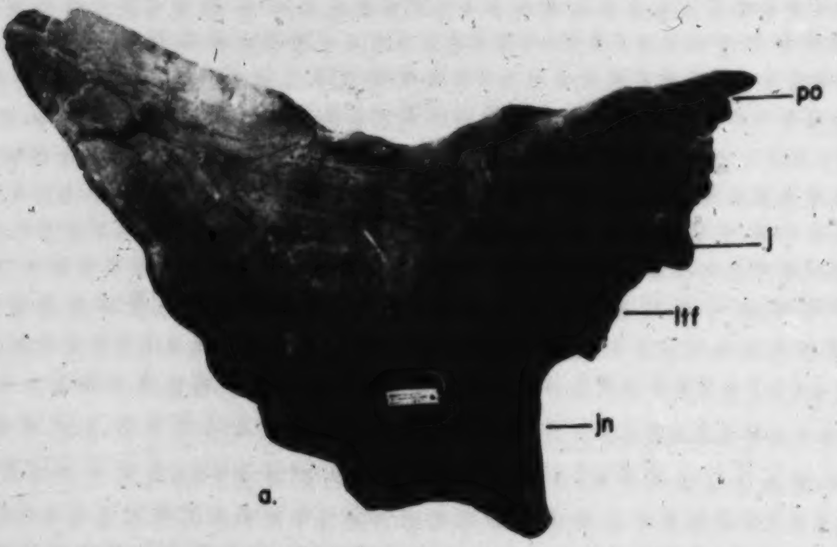
[1] Lambe (1914a) originally placed "Ceratops" belli in the genus Protorosaurus but later, when he discovered that Protorosaurus was preoccupied, he established the genus Chasmosaurus for the reception of this species.

[2] The status of the genus Monoclonius is discussed in a later section. Whether or not Monoclonius is a valid taxon, the material assigned by Lambe (1915) to Eoceratops is sufficiently distinct from the material assigned to Monoclonius (see below) to warrant the change in designation.

The ventral edge of the squamosal of NMC 1254 carries a series of projections, which are short and prominent anteriorly, long and low posteriorly. The most anterior of these projections lies immediately behind the jugal notch. A distinct change in texture separates the rugose lateral surface of this projection from the smooth surface of the rest of the squamosal. Although there is no trace of a suture at the base of this, or any other projection on NMC 1254a, the abrupt change in surface texture strongly suggests that this anterior projection is a large, coössified epoccipital. The next four more posterior projections also have rugose surfaces that contrast with the smooth surface of the rest of the squamosal, but on these, the two textures merge gradually into each other, with no sharp demarcation. Perhaps the process of coössification moved anteriorly with time and the four projections, if they are indeed epoccipitals, fused with the squamosal while the suture at the base of the most anterior epoccipital still was open, thereby accounting for the fact that a clear change in texture is visible only on the anterior projection. The last two projections are mere undulations of

Fig. 1. Right squamosal (NMC 1254a) of type specimen of *Eoceratops canadensis*, x.20. a. Lateral view showing sutural surfaces for postorbital (po), jugal (j), jugal notch (jn), and lateral temporal fenestra (ltf). b. Medial view showing sutural surfaces for quadrate (q), parietal (p) and exoccipital (ex).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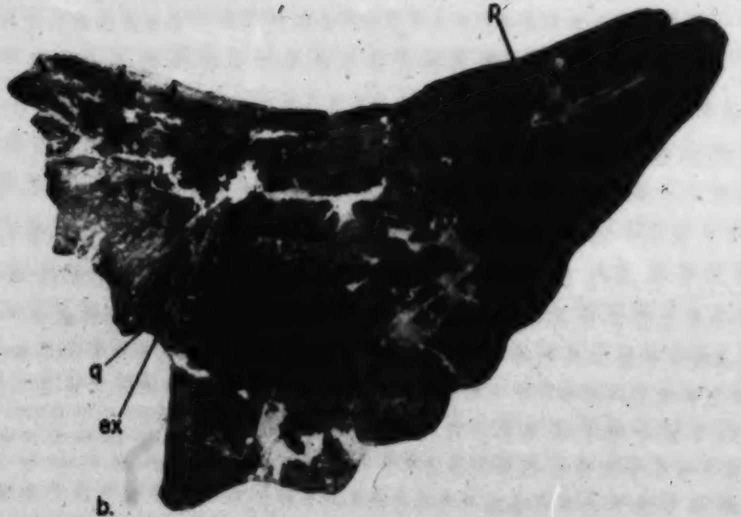
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the edge of the squamosal, with a rugose texture that is shared by the rest of the posterior part of this element. These could represent completely coössified epoccipitals presumably, although it seems more likely that they never were separate ossifications. If the rugose texture indicates a keratinous covering in life, however, as Hatcher, Marsh and Lull (1907) suggested, these posterior projections may have supported keratinous "epoccipitals".

When considering the ceratopsid specimen UA 40, both Gilmore (1923) and Lull (1933) noted the presence of epoccipitals, which they believed were not present in the type specimen of Eoceratops canadensis. (This supposed difference, in fact, was one of the reasons why Gilmore (1923) only provisionally assigned UA 40 to the genus Eoceratops.) If the projections on the ventral edge of the squamosal of the type specimen are coössified epoccipitals, however, then the only difference between UA 40 and NMC 1254a in this feature is the degree of fusion of the epoccipitals onto the frill. Examination of the sutures of the two specimens of Eoceratops (see below) indicates that NMC 1254 is a relatively younger individual than UA 40. Since the epoccipitals of UA 40 are distinct elements, if the projections on the squamosal of the type have been interpreted correctly, the sequence of sutural closing between the epoccipitals and squamosal was somewhat different in the two specimens.

The anterior edge of the squamosal of NMC 1254 is complex. Ventrally, there is a vertical, slightly thickened edge that represents the posterior border of the jugal notch. Dorsal to this edge lies a small part of the posterior edge of the lateral temporal fenestra, which separates the jugal notch from the complex sutural surfaces for the reception of the jugal and the postorbital.[1]

Posteriorly, the squamosal is short, blunt and thick but more anteriorly, the dorsal edge of the bone is thin, since the medial surface is excavated for the reception of an elongate anterior extension of the parietal. Anterior to this extension the squamosal thickens again, forming a series of bony ridges and knobs along its dorsal surface. (Lambe (1904a) felt that the smallest and most posterior of these embellishments might have been an area of muscle attachment but according to the present reconstruction (see below), all these structures are too far removed from the supratemporal fossae to have performed such a function.) Immediately anterior to the most posterior knob there is a deep but narrow groove, which deepens antero-medially to join a larger groove on the dorso-medial surface of the squamosal, although it persists for only a short distance on the lateral surface of the squamosal. Lambe (1904a, 1904b)

[1] In the area occupied in most reptiles by the postorbital and postfrontal bones, in ornithischians there is a single, large ossification (Romer 1956). There is no evidence to indicate whether this bone represents the postorbital, postfrontal or a combination of both. Since Romer (1956) has labelled this element the "postorbital", for the sake of consistency, it is labelled postorbital here, as well.

described this groove in some detail but offered no explanation of its function. From the narrowness of the groove, and its sinuous path, it appears likely that in life it held a large blood vessel. (A similar but less pronounced groove lies in approximately the same position on UA 40.)

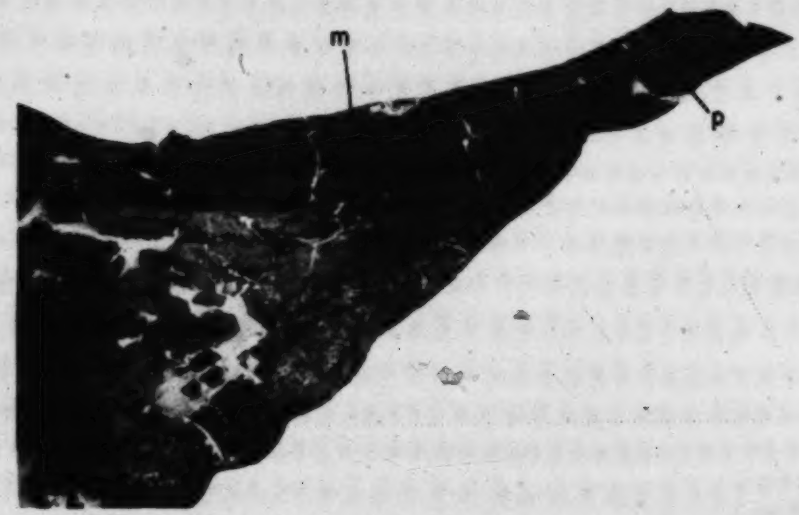
Anteriorly, the dorsal edge of the squamosal of the type specimen forms a horizontal platform, the posterior edge of which lies immediately above the thickest portion of the squamosal. Anteriorly, the entire dorsal surface of the squamosal becomes increasingly rugose and the horizontal platform supports three conspicuous ridges, as well. The anterior ridge ends in a rugose peg that forms part of the sutural surface for the postorbital.

The lateral surface of the squamosal is relatively smooth, except for continuations of the ridges from the dorsal edge. Posteriorly, the lateral surface is concave but elsewhere it lacks distinct topographic features. The medial surface is more complex (Fig. 1b). Above the posterior edge of the jugal notch is a deep, triangular depression that housed the proximal head of the quadrate. Thick ridges on either side of this depression braced the quadrate further and the thickest and most posterior ridge also has a slight central depression for the reception of the lateral edge of the exoccipital. This arrangement is typical of ceratopsids, ensuring that no movement of the quadrate with respect to the rest of the skull would have been possible. Anterior to these features, the medial surface is deeply excavated, bearing grooves and depressions that formed a complex sutural surface for the postorbital.

The only part of the parietal that is preserved in the type specimen is a long, anterior extension of the right side. This element (NMC 1254b) is roughly triangular, articulating with a deep groove on the dorso-medial surface of the squamosal (Fig. 2). When articulated, the end of the parietal projects beyond the posterior edge of the squamosal and when complete, it must have projected even further. Whereas the lateral surface of NMC 1254b is flat and articulates smoothly with the squamosal, a prominent ridge extends along the medial surface, separating a broad ventromedial area from a more narrow dorsal area.

Lambe (1904*a*, 1915) felt that the frill fenestrae of this individual (NMC 1254) differed from those of other ceratopsids in having part of the lateral boundary formed by the squamosal, instead of the entire fenestra lying within the coalesced parietals. (Only the lateral edge of the right frill fenestra of NMC 1254 is preserved.) In form, the anterior portion of the squamosal and the preserved portion of the parietal of NMC 1254 are very similar to the corresponding elements in *Chasmosaurus* and *Pentaceratops* and probably the shape of the complete fenestra also was similar to that of *Chasmosaurus* and *Pentaceratops*. In *Centrosaurus*, *Styracosaurus*, *Arrhinoceratops* and *Anchiceratops*, the

Fig. 2. Right squamosal (NMC 1254a) and anterior extension of right parietal (NMC 1254b) of type specimen of *Eoceratops canadensis*, showing the posterior projection of the parietal (p) and the medial ridge on the parietal (m). x.20.


m
p

fenestrae[1] lie entirely within the parietals. In the long-squamosaled genera Chasmosaurus and Pentaceratops, however, the lateral parts of the parietal are extremely narrow, forming thin, anterior extensions that lie almost directly beneath the dorsal edge of the squamosal, so that the squamosal participates in the lateral border of the fenestra. Nonetheless, in both Chasmosaurus and Pentaceratops, given a complete parietal but no squamosal, it still would be possible to define the shape of the fenestrae exactly. Futhermore, based on the similarity between Chasmosaurus and Eoceratops, presumably one could define the frill fenestrae of Eoceratops in the same way, if the entire parietal were known. By this criterion, therefore, the frill fenestrae in all ceratopsids lie wholly within the parietals and any differences with respect to the position of the squamosal are merely differences of proportion that do not reflect fundamentally different patterns of development.

The similarities between the squamosal and the preserved part of the parietal of NMC 1254 (Eoceratops) and comparable parts of the frills of Chasmosaurus and Pentaceratops are quite extensive. In both Chasmosaurus and Pentaceratops the basic shape of the squamosal is triangular, as in *Eoceratops*, although the posterior extent of this element is much greater than in *Eoceratops*. There is a distinct change in the slope of the dorsal border of the squamosal, as in *Eoceratops*, with the short, anterior portion being more or less horizontal and the long, posterior portion being strongly inclined dorsally. The lateral surface of the squamosal is concave, although this concavity is relatively larger and deeper than in *Eoceratops*, owing to the greater extent of the dorso-medial excavation supporting the anterior extension of the parietal. (This dorso-medial excavation is reflected on the lateral surface by a thick ridge, forming the dorsal border of the lateral concavity, so that a deeper excavation on the medial surface results in a larger ridge, and a relatively deeper lateral concavity.) Also, the anterior extension of the parietals of *Chasmosaurus* and *Pentaceratops* closely resembles that of *Eoceratops*. Therefore, despite the fact that the frill of NMC 1254 is incomplete, the presence of so many features that are similar to comparable parts of *Chasmosaurus* and *Pentaceratops* indicates that the complete frill of *Eoceratops* probably was similar to those of the long-squamosaled genera; it likely had elongate fenestrae, completely surrounded by the parietals but with the lateral part of the parietal so attenuated that the squamosal would lie adjacent to the frill fenestra. Although the exact extent of the parietal posterior to the squamosal is unknown in *Eoceratops*, comparisons with *Chasmosaurus* and

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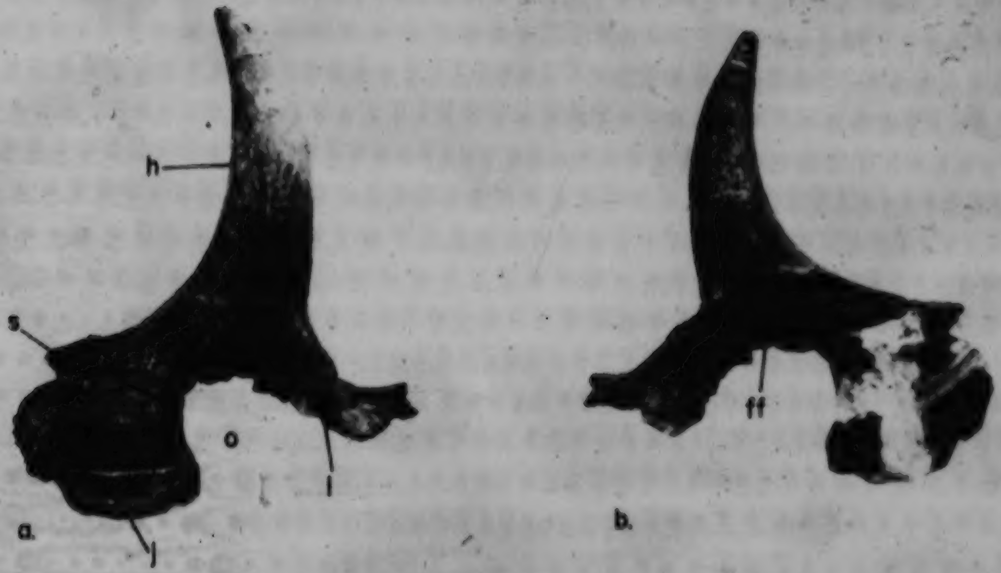
[1] This discussion concerns only the main, paired frill fenestrae that are present in all ceratopsids except Triceratops. Supernumerary fenestrae, which may occur in either squamosal or parietal and are unpaired and variably distributed, are discussed in a later section.

Pentaceratops suggest that the parietal formed a thick bar that projected only slightly beyond the posterior edge of the squamosals.

The anterior, as well as the posterior edge of the parietal of NMC 1254 is broken, so that the anterior boundary of the frill fenestra is missing. (Lambe (1915) apparently considered the broken anterior end of the parietal to be the farthest anterior extent of this element, although he did not discuss the anterior boundary of the frill fenestra.) Based on the similarities between the preserved parts of the frill of the type specimen and the frills of *Chasmosaurus* and *Pentaceratops*, it seems likely that the more anterior parts of the parietals also were similar in these genera and *Eoceratops*. If this assumption is correct, the parietal of *Eoceratops* would have formed a thin, broad plate, extending forward from the anterior edge of the frill fenestra to form the floor of the supratemporal fossa. Medial to the fossa, the parietal would have formed a thickened, rugose, shield-like area, thinning posteriorly at the medial borders of the two frill fenestrae and finally joining the posterior bar mentioned above. This assumption is supported by comparisons between the type specimen of *Eoceratops canadensis*, *Chasmosaurus*, *Pentaceratops* and UA 40 (see below).

The element that contains most of the orbit and the brow horn core of the type specimen of *Eoceratops canadensis* (NMC 1254d) (Fig. 3a, b) was described by Lull (1933, p.91)

Fig. 3. Right postorbital, frontal and prefrontal (NMC 1254d) of type specimen of Eoceratops canadensis, x.20. a. Lateral view showing orbit (o), brow horn core (h), and sutural surfaces for lacrimal (l), jugal (j) and squamosal (s). b. Ventromedial view showing frontal fossa (ff).


h
s
o
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a.
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as "the right postfrontal and prefrontal". As mentioned above, the "postfrontal" is termed here the "postorbital" and whereas the prefrontal is present in this specimen, parts of the frontal almost certainly are present, as well. (In all ceratopsids, the area between the anterior part of the frill and the brow horn cores often is difficult to interpret because of sutural fusion.)

In NMC 1254, the orbit is oval, with the long axis vertical. The brow horn core arises immediately dorsal to the orbit, the rim of the orbit continuing smoothly into the lateral surface of the horn core and the base of the horn core lying almost directly above the anterior edge of the orbit. Although its base is robust, the horn core tapers rapidly to a narrow tip, with a circular cross section for most of its length but a basal cross section that is slightly compressed laterally. The horn core is upright and recurved; at its base there are a few deep vascular marks but most of its surface is relatively smooth.

Lambe (1915) and other authors have suggested that the size and shape of the brow horn cores of ceratopsids have taxonomic significance. Certainly, one can define trends in this feature: Centrosaurus, for instance, has extremely short, triangular brow horn cores while those of Pentaceratops are extremely long, tapering distally to a sharp point. Nonetheless, the precise configuration of the horn cores does not seem to be of great taxonomic importance, at least at the generic level. Chasmosaurus *kaiseni* has long, tapering brow horn cores quite similar to those of *Eoceratops*, but *Chasmosaurus belli* and *C. brevirostris* have short, triangular horn cores, more similar to those of *Centrosaurus* than to *Chasmosaurus kaiseni*. An attempt to place *Chasmosaurus belli* and *C. brevirostris* in the genus *Centrosaurus* on the basis of this similarity, however, would be ridiculous in view of the rest of the features of the skull, which are very different from those seen in *Centrosaurus*. (*Chasmosaurus russelli* apparently lacks brow horn cores altogether, although the bone above the orbital rim is thick and rugose and may have supported a keratinous sheath (Sternberg 1940).) In ceratopsids, the brow horn cores often show considerable post-mortem distortion, as in UA 40, or distortion due to disease or injury, as in the left horn core of NMC 2280 (*Chasmosaurus belli*), making variation in this structure even less useful as a taxonomic character. Thus, the features cited by Lull (Hatcher, Marsh and Lull 1907) differentiating "*Ceratops*" (=*Eoceratops*) *canadensis* from *Ceratops montanus* are not of taxonomic significance. Nor can meaningful comparisons, allowing the assignment of further material to the genus *Ceratops*, be made on the basis of the brow horn cores of the type species, *C. montanus*.

The brow horn cores of *Eoceratops* are formed, as in all ceratopsids, by the postorbital. Posterior to the brow horn cores, the postorbital has a ventral flange with distinct sutural surfaces for the jugal, ventrally, and the squamosal, posteriorly. The anterior edge of this flange forms part of the edge of the orbit. Much of the medial surface of the postorbital of NMC 1254 (Eoceratops) (Fig. 3b) is covered by a plaster support but anteriorly, one can distinguish part of the frontal fossa, which in life would have lain between the braincase and a secondary roofing formed by the frontals and postorbitals. The fossa appears to have been large in Eoceratops, although only the right lateral wall is preserved in the type specimen. This wall contains three major depressions: a large, deep posterior concavity, lying immediately posterior to the brow horn core, and two shallower, anterior concavities, lying directly beneath the horn core and separated from the posterior concavity by a prominent ridge.

Lambe (1915, p.5) described the prefrontal of the type specimen of Eoceratops as a small element bounded "outwardly on two of its sides ... by the postfrontal." A white line has been drawn on the dorsal surface of NMC 1254d to indicate the extent of the prefrontal, according to Lambe's interpretation. This line follows a deep, irregular groove in the surface of the bone but it seems unlikely that this groove represents a suture and more probably, Lambe's "suture" is a crack caused by post-mortem crushing. Lambe's interpretation requires an anterior extension of the "postfrontal" (postorbital) to project between the prefrontal and lacrimal, so that these two latter elements do not meet. I am not aware of a similar condition in the skull of any other reptile and since there are clear indications of a sutural surface for the lacrimal on the ventral edge of this "postfrontal" extension, the groove cannot represent part of the prefrontal-lacrimal suture either. Given the improbability of an anterior extension of the "postfrontal", as postulated by Lambe (1915), the fact that the prefrontal sutures generally are obliterated in ceratopsids, at least posteriorly, and the fact that the sides of this "suture" have a rough, broken appearance, probably this groove is a crack and the postorbital, frontal and prefrontal sutures have been obliterated by coössification.

Lambe (1915) figured and described a rough surface on the anterior edge of the orbit as part of the sutural surface for the lacrimal but there is also a smooth, thin sutural surface on the ventral edge of the prefrontal, anterior to this roughened area, which contributed to the prefrontal-lacrimal suture. The position of this suture corresponds to the position of the prefrontal-lacrimal suture in UA 40, and in other ceratopsids where this suture is visible.

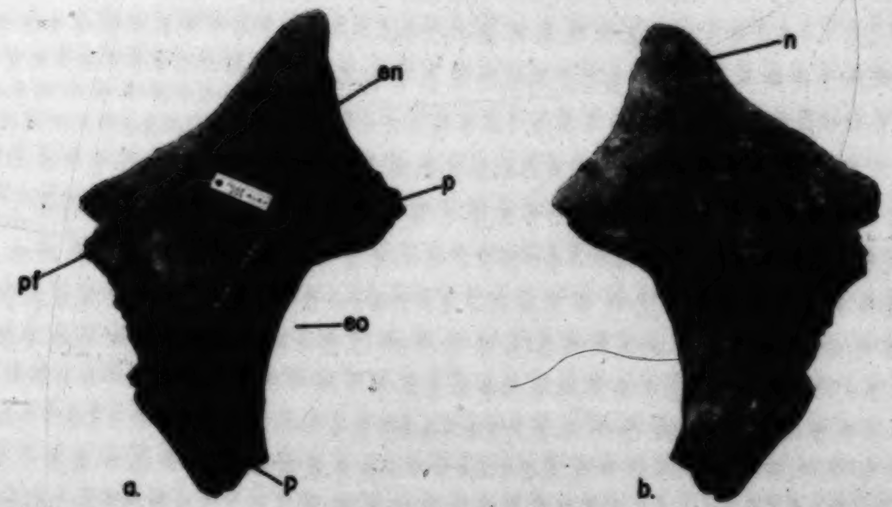
Most, perhaps all, ornithischian dinosaurs possess palpebral (=supraorbital; supraciliary) ossifications, small bones of variable size and shape lying in the dorsal portion of the orbit (Coombs 1972). There is a single, large palpebral projecting into the antero-dorsal portion of the orbit of psittacosaurids (see Coombs 1972, fig. 3B) but in both protoceratopsids and ceratopsids, the palpebrals are relatively small. (In protoceratopsids, this element articulates loosely with the prefrontal, a situation found elsewhere among ornithischians only in the ornithopods (Coombs 1972).) According to Coombs (1972, p.643), the "presence of a palpebral in ceratopsids is equivocal." In some cases, UA 40, for example, there is a distinct elevation on the anterior edge of the orbit that clearly represents a palpebral bone fused into the lacrimal, prefrontal and postorbital ossifications. More often, if a palpebral ossification is present, it has fused smoothly into the rest of the orbital rim. Since distribution of this element is erratic within the Reptilia (Coombs 1972), it is possible that not all ceratopsids possess a palpebral bone but since palpebrals are present in psittacosaurids, protoceratopsids and some ceratopsids, these elements probably are present in all ceratopsids, although they are more prominently developed in some species. Certainly, the presence of palpebral ossifications appears to be a primitive character for the Ceratopsia.

Even where fused into the antorbital region, palpebrals would serve to strengthen the anterior rim of the orbit, an area that undoubtedly was subjected to large stresses (see below). In the type specimen of Eoceratops canadensis, there is a slight thickening where one would expect a palpebral ossification, although this thickening is not as prominent as in UA 40. Probably this feature exhibits considerable individual variation, the exact shape being less important than the function of thickening and bracing the orbital rim.

Not all the sutures bounding the prefrontal of NMC 1254 (*Eoceratops*) are fused; anteriorly, there is a deeply notched surface for the reception of the nasal. Part of the nasal (NMC 1254c) articulates with this surface but the rest of the prefrontal-nasal suture, and all of the lacrimal-nasal are lost (Fig. 4a, b).

The nasal horn core of the type specimen is short and triangular in outline, arising above the posterior edge of the external narial opening. Lull (1933, p.91) stated that "the skull [of NMC 1254] ... differs from all other Belly River genera in the nature and position of the nasal horn core. The character may be partly juvenile, but the position over the forward margin of the narial opening, instead of over the rear, separates it from *Monoclonius* (*Centrosaurus*), *Chasmosaurus*, and *Styracosaurus*, and likens it to the Lance *Triceratops*." In making this statement, Lull seems to have been influenced heavily by Lambe's (1915, pl. I) restoration of *Eoceratops*, in which the nasal element has been rotated anteriorly so that the nasal horn core lies above the (restored) anterior rim of the external narial opening. Although the prefrontal and nasal of NMC 1254 can be articulated, the edges of the sutural surfaces are broken and the fit is not exact. Thus, the neat fit shown by Lambe (1915) is misleading and the nasal horn core probably was more upright than in his restoration. Comparison with UA 40,

Fig. 4. Right nasal (NMC 1254c) of type specimen of Eoceratops canadensis, x.25. a. Lateral view showing external narial opening (eo), and sutural surfaces for epinasal (en), premaxillary (p) and prefrontal (pf). b. Medial view showing sutural surfaces for opposing nasal (n).


en
p
pf
eo
p
a.
n
b.

which has an extremely similar nasal region, also indicates a more upright orientation, placing the nasal horn core over the posterior edge of the external narial opening, as in most other ceratopsids. (Lambe's (1915) restoration of the premaxillary probably is incorrect as well, since it places the anterior edge of the external narial opening in a more posterior position than is indicated by UA 40.)

The anterior edge and much of the lateral surface of the nasal horn core of NMC 1254 support a large, highly rugose surface for the reception of a separate epinasal ossification. Slighty below the apex of the horn core a small fragment of the epinasal is preserved, throughly fused to the underlying nasal, but no other portions of the epinasal are evident, indicating that coössification of the nasal and epinasal took place gradually and did not involve the entire sutural surface at one time. When complete, the epinasal must have been a relatively large element as the sutural surface extends from the dorsal tip of the horn core to the articular surface that received the dorsal process of the premaxillary. The shape of the sutural surface and the presence of a median suture in the nasal horn core indicate that the epinasals were paired. The median sutural surface is incomplete ventrally but, when complete, it would have extended from the tip of the horn core to the level of the dorsal edge of the external narial opening. Beneath this sutural surface, the nasal is deeply concave and the bone is much thinner. The anterior edge of this concave surface forms part of the edge of the external narial opening.

At the anterior edge of the sutural surface for the epinasal there is a short, rounded articular surface for the reception of the dorsal process of the premaxillary. Ventrally, the nasal of Eoceratops has two stout projections that articulate with a strong posterior projection of the premaxillary so that together, the nasal and premaxillary surround the external narial opening. The ventral nasal-premaxillary suture is much more complex than the dorsal nasal-premaxillary suture, which is a simple scarf joint (see below). The ventral edge of the nasal forms two narrow processes: the anterior one overlaps part of the postero-dorsal premaxillary process, while the broader, posterior process underlies this same structure. In NMC 1254, a distinct ridge on the posterior process marks the limit of the overlap between these two bones. (The ventral edge of the anterior process is broken in NMC 1254 but when complete, the two processes probably were the same length, as they are in UA 40.) This overlapping articulation ensured a strong ventral union between the nasal and premaxillary, whereas the dorsal articulation between these two elements was not as strong.

In the original description of "Monoclonius" (=Eoceratops) canadensis, Lambe (1902, p.63) referred to, but neither described nor figured, "some other parts of the skull [of NMC 1254], not yet fully determined". These elements are not described in anysubsequent paper dealing with this specimen and in 1915, when Lambe listed the type material for *Eoceratops canadensis*, he did not mention these "other parts". Included with the type material of *Eoceratops canadensis* is a small, roughly diamond-shaped element bearing the same catalogue number (NMC 1254), taxonomic designation and collector's name as the rest of the type material (Fig. 5a, b). It is possible that this element is part of the "other" material referred to by Lambe (1902), although it does not appear to be part of the skull and it is too incomplete to be identified.

The only other part of the head skeleton of the type of *Eoceratops* that is preserved is the left dentary (NMC 1254e) (Fig. 6a, b). This element is deep and robust, with a strongly developed coronoid process that is marked by a distinct anterior hook, and a ventral edge that is slightly convex, although not to the degree seen in older individuals of *Protoceratops*. No teeth remain in the jaw and neither the predentary nor any of the post-dentary bones are preserved.

A partially restored presacral vertebra (NMC 1254) (Fig. 7a, b) is the only part of the postcranial skeleton known for the type specimen of *Eoceratops canadensis*, with the possible exception of the ?postcranial fragment described above. Lambe (1902) identified this vertebra as an anterior dorsal but there is some dispute as to the assignment of posterior "cervicals" and anterior "dorsals" in ceratopsids. Hatcher (Hatcher, Marsh and Lull 1907, p.47) distinguished cervical from dorsal vertebrae in ceratopsids

Fig. 5. ?Postcranial fragment (NMC 1254) of type specimen of *Eoceratops canadensis*, x.45. a. "Dorsal" view. b. "Ventral" view.

a.

b.

Fig. 6. Left dentary (NMC 1254e) of type specimen of Eoceratops canadensis, x.3. a. Lateral view showing coronoid process (cp). b. Medial view showing inframandibular canal (ic).

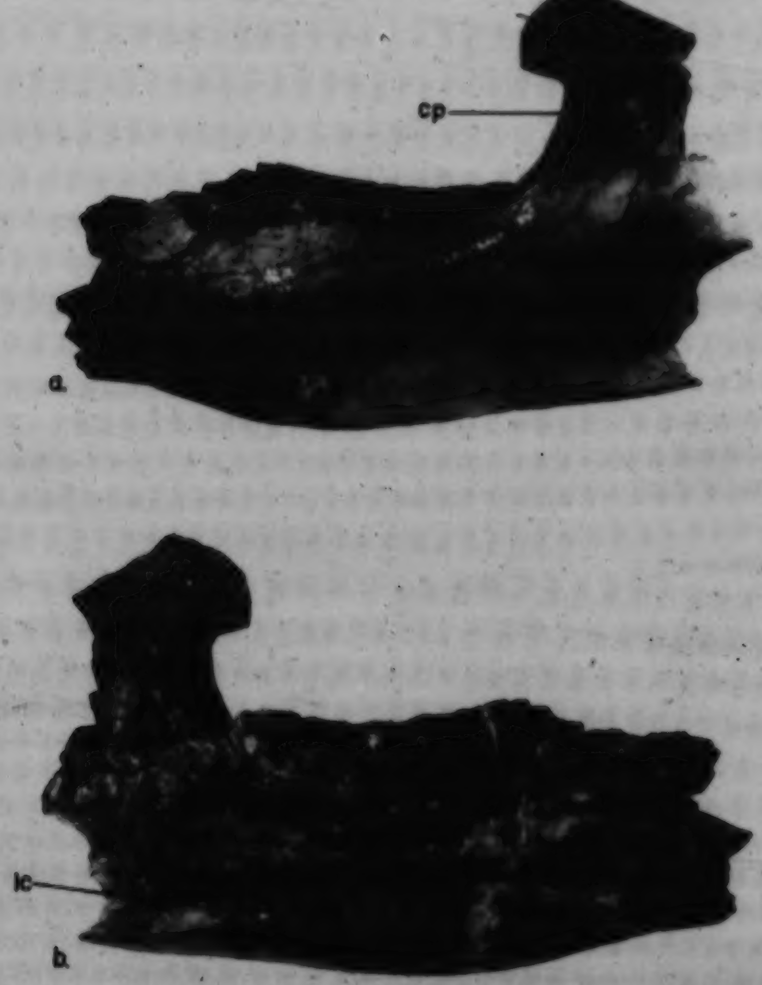
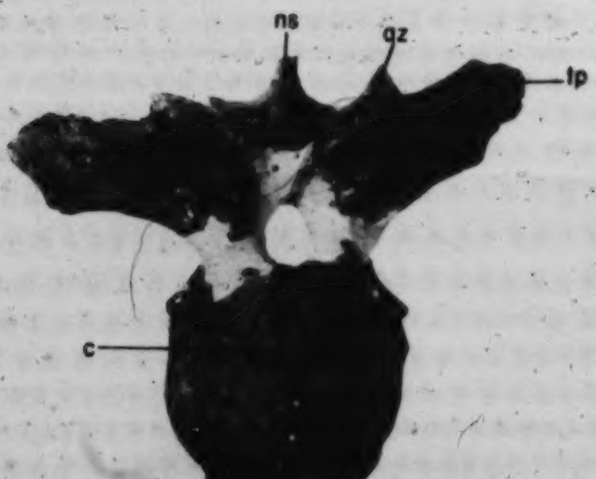
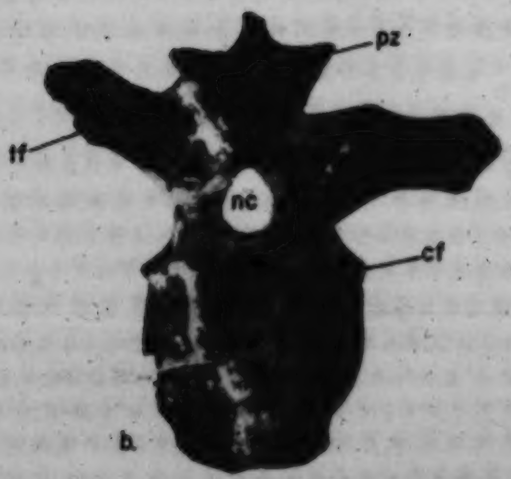

cp
a.
lc
b.

Fig. 7. Anterior dorsal or posterior cervical vertebra (NMC 1254) of type specimen of *Eoceratops canadensis*, x.35. a. Anterior view showing anterior zygapophysis (az), base of neural spine (ns), transverse process (tp) and centrum (c). b. Posterior view showing posterior zygapophysis (pz), neural canal (nc), tubercular facet (tf) and capitular facet (cf).


ns
az
tp
c
a.


pz
tf
nc
cf
b.

"not so much by differences in the vertebrae themselves as by the differences in the ribs which they support", cervical ribs being straight and thoracic ribs being strongly curved, and he maintained that this criterion applied to "all herbivorous dinosaurs". Brown (1917, p.288), however, felt that "in the cervical series throughout the Dinosauria [sic] the capitular facets are invariably located on the centra of the vertebrae, the change from the cervical to the dorsal series being marked by the rise of this facet from the centrum to the neural arch." As the two series of vertebrae grade into each other, and both form of ribs and position of capitular facets change gradually, the distinction between dorsal and cervical is rather arbitrary. No rib is preserved with NMC 1254, so it is not possible to apply Hatcher's criterion but by Brown's definition, this vertebra belongs to the posterior cervicals, as the capitular facet is on the dorsal edge of the centrum. Whatever the terminology, by analogy to other ceratopsids in which the vertebral column is complete, this vertebra was approximately ninth in the column, counting the three coalesced anterior cervicals as I, II and III. (Lambe (1902, fig. 19) illustrated but did not describe this vertebra, nor was it described in subsequent papers dealing with NMC 1254.) The neural spine is broken but the orientation of its base indicates that the spine was more or less vertical. The centrum is biconcave, although the anterior surface is only very slightly concave, and the sides and base of the centrum are excavated, although not to such a degree that this vertebra could be termed pleurocoelous. The neural canal is partially restored but enough of the posterior edge of the canal remains to show that it was large, again indicating the relatively anterior position of the specimen, since the cervical vertebrae are characterized by large neural canals (Lull 1933).

(b) Description of UA 40; comparison with NMC 1254

All the cranial elements known for NMC 1254, except the anterior extension of the parietal, are present in UA 40 (Fig. 8a, b) and in all comparable parts the two specimens are extremely similar, supporting Gilmore's (1923) assignment of UA 40 to the genus Eoceratops.

The squamosal of UA 40 is incomplete posteriorly, lacking much of the posterior edge. From comparison with AMNH 5401 (Chasmosaurus kaiseni), Lull (1933, pl. VIIB) restored the missing parts of the squamosal on UA 40 as a long posterior extension, longer than the portion actually present. As Lull recognized in doing this, the squamosal of UA 40 is similar to that of Chasmosaurus kaiseni; but it is also very similar to that of Eoceratops (NMC 1254), with the main difference between the frills of Eoceratops and Chasmosaurus kaiseni, as far as is known, being the extent of the posterior portion of the squamosal. The squamosal of UA 40 may have had a long posterior extension, as in

Fig. 8a. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), x.22.

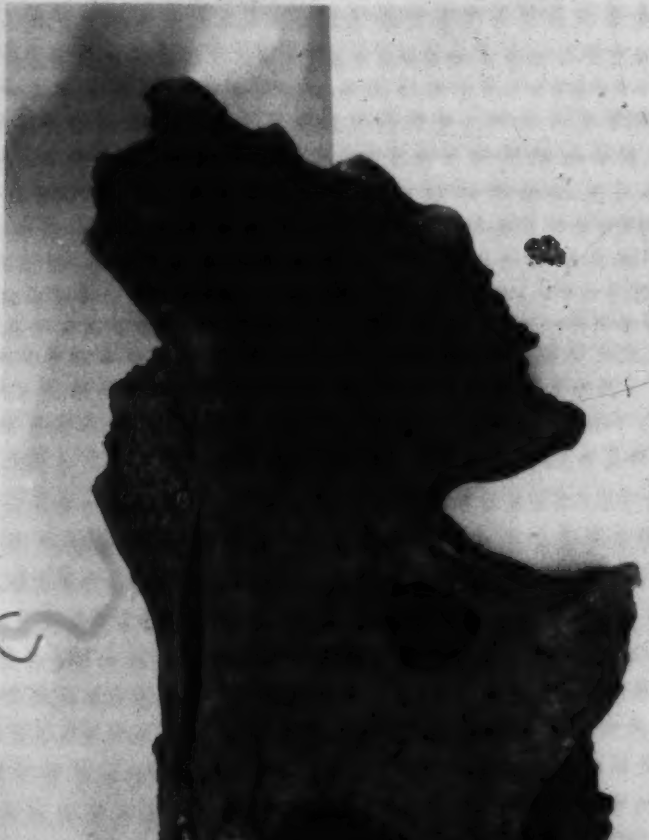
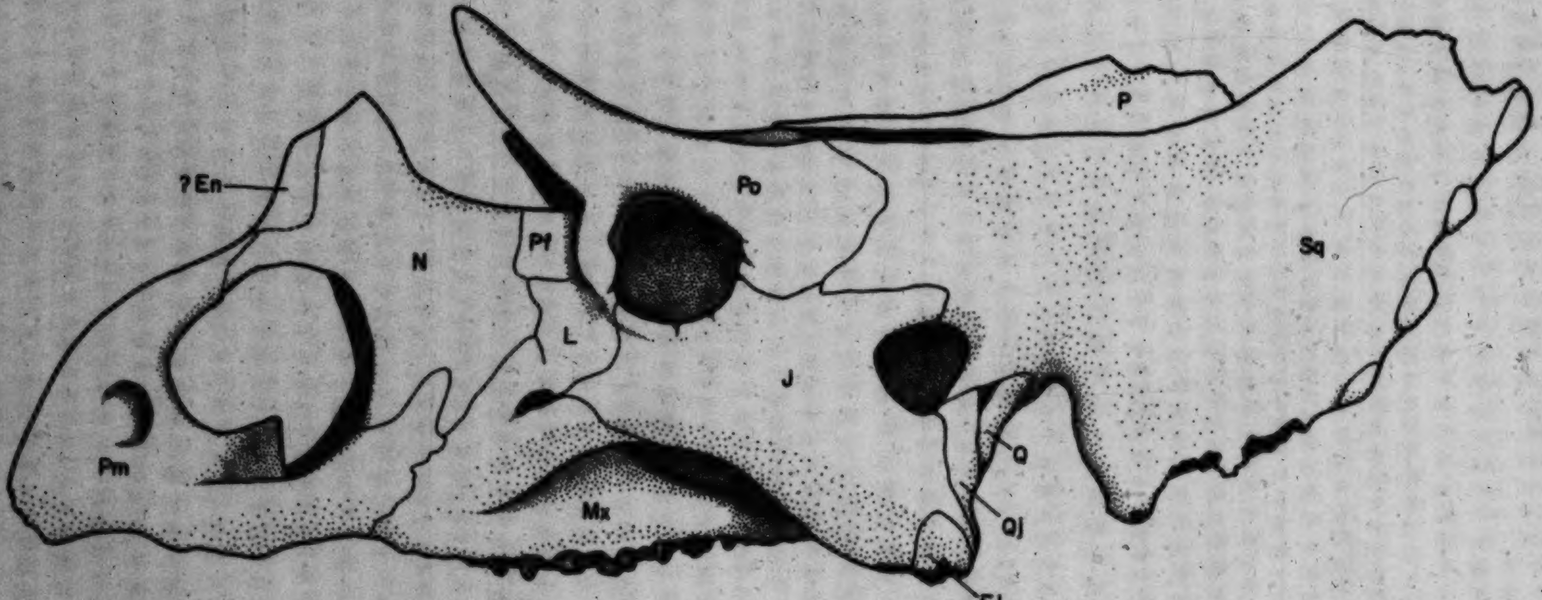


Fig. 8b. Left lateral view of skull of UA 40 (Eoceratops canadensis), x.22. (For abbreviations for this, and all subsequent drawings, see "Table of Abbreviations" on p.xvii.)


P
?En
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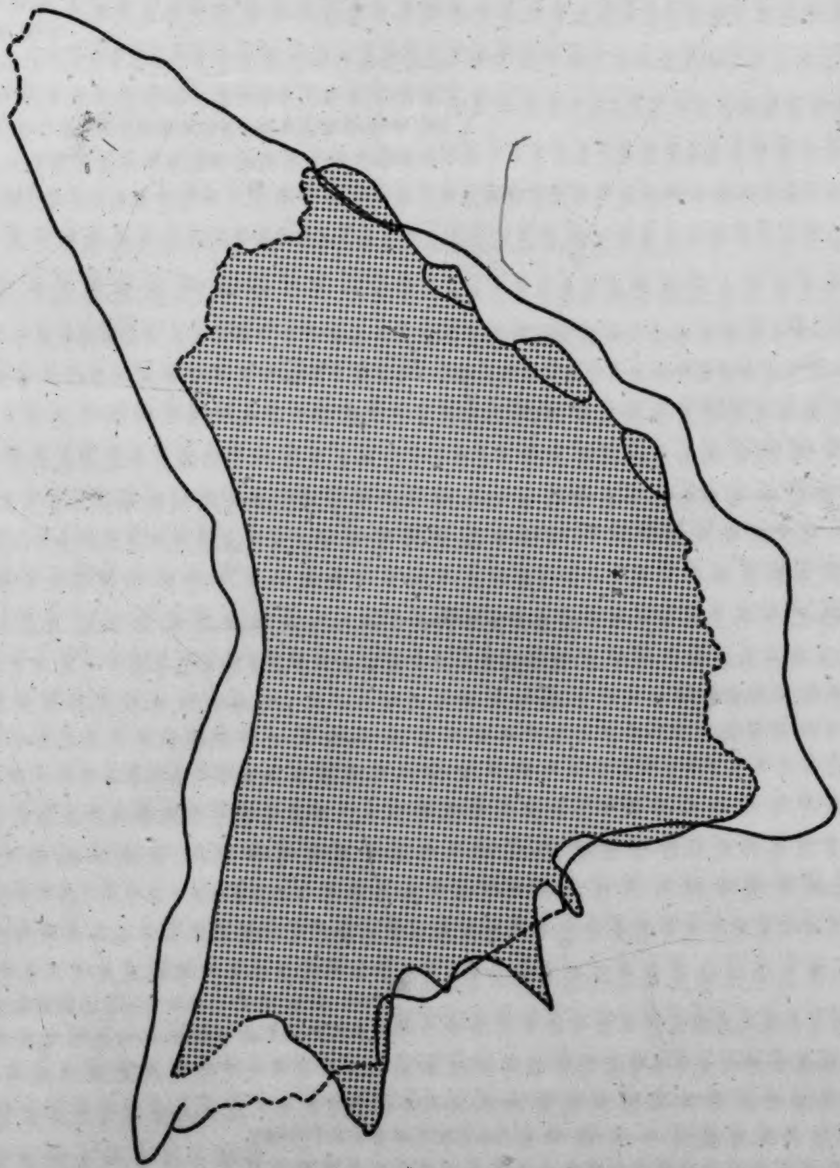
Qj
Ej

Chasmosaurus kaiseni, but anteriorly it is relatively deeper than in *C. kaiseni*, closer to that of *Eoceratops*; and what is present of the squamosal-postorbital suture is also somewhat closer to the condition seen in *Eoceratops*. In all known specimens of *Chasmosaurus*, as in *Eoceratops*, the epoccipitals are completely fused to the squamosal, forming mere undulations of the ventral surface rather than separate ossifications, so the character of the epoccipitals of UA 40 does not debar this specimen from *Eoceratops* any more than from *Chasmosaurus*. Therefore, since there is no positive evidence of a long posterior extension of the squamosal of UA 40, and since the squamosals of UA 40 and NMC 1254 are very similar, I have restored UA 40 with a short squamosal, as in the type specimen of *Eoceratops canadensis*.

The squamosals of both UA 40 and NMC 1254 (Fig. 9) show a distinct change in the slope of the dorsal surface and the general outline is similar except in areas of breakage or, in UA 40, where the sutures have been obliterated. Both show a relatively small lateral temporal fenestra (in a more dorsal position than in other ceratopsids), a large jugal notch and a thickened postero-dorsal ridge that presumably is correlated with an elongate anterior extension of the parietal in both individuals. Both specimens show distinct ridges on the dorsal edge of the squamosal although these ridges are fewer in number and less prominently developed in UA 40. Except for the squamosal-epoccipital sutures, however, the sutures bordering the squamosal of UA 40 are

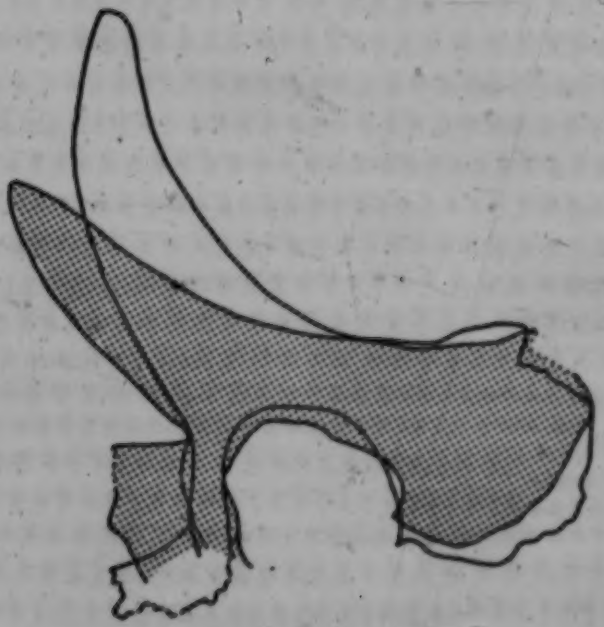
Fig. 9. Right squamosal (NMC 1254a) (image reversed) of type specimen of *Eoceratops canadensis* superimposed upon the left squamosal of UA 40 (*E. canadensis*), x.29. (UA 40 - stipple; broken edges - dashed lines.)



closed, whereas in NMC 1254, even though the squamosal is larger than that of UA 40, these sutures are open, indicating a younger individual. (Such differences in size and ornamentation may be due to individual variation, sexual dimorphism or different taxonomic relationships but with such a limited number of specimens, one cannot estimate the taxonomic importance of these variations.) UA 40 also shows a rough, flattened area, almost circular in outline, on the dorsal edge of the squamosal, which is not present in NMC 1254 but this area probably is pathologic in origin (see below) so that its absence in NMC 1254a is not significant.

Both Gilmore (1923) and Lull (1933) mentioned the difference in orientation of the brow horn cores of UA 40 and NMC 1254, although neither author considered this difference important. The area anterior to the brow horn cores in UA 40 is badly crushed so that the horn cores would have been more nearly upright in life, as in NMC 1254d, and when restored in this more upright position, the brow horn cores of UA 40 arise above the anterior rim of the orbit, as in NMC 1254. Probably, there was individual, sexual and ontogenetic variation in the shape and inclination of the brow horn cores of ceratopsids, as there is in modern bovids, so minor variations in the horn core should not be considered taxonomically important. The shape and proportions of the horn cores and of the postorbital-prefrontal region are very similar in UA 40 and NMC 1254d (Fig. 10), again, the apparently great differences

Fig. 10. Right postorbital, frontal and prefrontal (NMC 1254d) (image reversed) of type specimen of Eoceratops canadensis superimposed upon the left postorbital, frontal and prefrontal of UA 40 (E. canadensis), x.27. (UA 40 - stipple; broken edges - dashed lines; coossified sutures - dotted lines.)



in the prefrontal region being caused by crushing. (Crushing between the brow horn cores also makes it impossible to describe the frontal fossa of UA 40.)

As mentioned above, the coössified palpebral of UA 40 is much more prominent than that of NMC 1254 but this difference is so small when compared to the overall similarity between these two specimens in this region that it is unlikely that it is of taxonomic significance.

As with the squamosal, the sutures of the postorbital-frontal-prefrontal area of UA 40 are closed to a greater degree than in NMC 1254, again indicating that UA 40 is an older individual.

Lull's (1933) main objection to assigning UA 40 to the genus *Eoceratops* was the presence of a longitudinal division of the nasal horn core in the type specimen of *Eoceratops canadensis*. There is no indication of such a division in UA 40 but considering that most of the other sutures in this skull are coössified to a greater degree than in NMC 1254, it does not seem unreasonable to postulate that a median suture was present in UA 40 at one time but was subsequently obliterated with age. This difference becomes, then, a matter of relative age rather than taxonomic distinction.

In defining *Eoceratops*, Lambe (1915) listed the presence of separate epinasal ossifications as one of the distinguishing characteristics of the genus but neither Gilmore (1923) nor Lull (1933) discussed these elements with respect to UA 40. Although most of the nasal horn core of UA

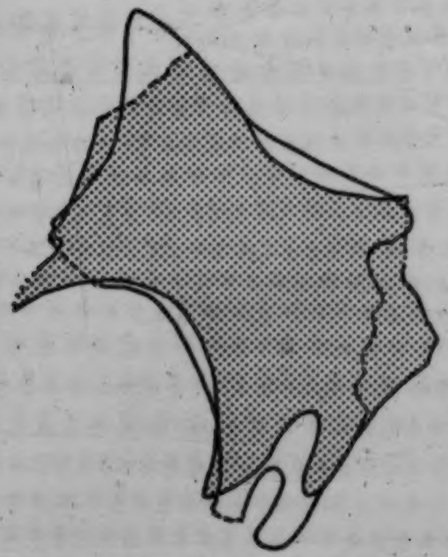
40 is fused solidly to the underlying nasal, part of an epinasal-premaxillary suture, as well as part of a suture between two epinasal ossifications, is preserved on the ventro-anterior edge of the horn core. Further, although most of the nasal horn core has a well preserved surface, anteriorly, on the left side, there is an area that is distinctly separate in texture and state of preservation from the rest of the horn core. Possibly, this poorly preserved area corresponds, at least in part, to the epinasal ossification of that side but unlike NMC 1254, the epinasals of UA 40 are almost completely fused to each other and to the underlying nasals.

Where preserved, the nasals of UA 40 and NMC 1254 are similar in shape and proportion although the nasal of the type specimen is slightly deeper and the dorsal edge is not as strongly curved (Fig. 11). In UA 40, the sutures bordering the nasal area are closed, the dorsal portion of the nasal-prefrontal suture being obliterated by coössification, whereas in NMC 1254 only the small extent of the nasal-epinasal suture mentioned above is closed.

The dentary of UA 40 is very poorly preserved and since variations in the dentaries of ceratopsids are slight, this element gives no indication of the relationship between UA 40 and NMC 1254.

The squamosal, postorbital-frontal-prefrontal region, the nasal and the dentary are the only elements present in both UA 40 and NMC 1254 and although there are slight

Fig. 11. Right nasal (NMC 1254c) (image reversed) of type specimen of *Eoceratops canadensis* superimposed upon the left nasal of UA 40 (*E. canadensis*), x.27. (UA 40 - stipple; broken edges - dashed lines; coossified sutures - dotted lines.)



differences in size and proportions, these elements are closely similar in the two specimens. Some elements resemble comparable regions of the skull of other genera, but no more so than NMC 1254; and taken together, the preserved parts of the type specimen of *Eoceratops canadensis* are morphologically closer to comparable parts of UA 40 than to any other specimen. Therefore, UA 40 is assigned without qualification to the genus *Eoceratops*. There are age differences between the two specimens and there are differences that may be due to age, sex or individual variation but, considering the restricted number of specimens of *Eoceratops* available for comparison, these do not seem sufficient reason to establish a separate species for UA 40 and therefore this specimen should be included in *Eoceratops canadensis*. Since the skull of UA 40 is much more complete than NMC 1254, the assignment of UA 40 to *Eoceratops* makes it possible to define the genus with much greater accuracy and there is now no reason to consider *Eoceratops* indeterminate.

Although the anterior extensions of the parietal have been destroyed by crushing in UA 40, the more medial parts of this element are preserved. The frill fenestrae, however, and the posterior parts of the frill of *Eoceratops* still are not known. The parietal of UA 40 is flat anteriorly along the midline, expanding and becoming strongly arched posteriorly. On each side of this rugose median section, thin smooth extensions of the parietal form the floor of the supratemporal fossae but crushing and coössification of sutures make it impossible to determine the anterior extent of the parietal here. Anteriorly, the parietal forms a broad but thin ledge that projects laterally over the fossa but more posteriorly, the parietal and the floor of the fossa meet in a distinct ridge. The anterior parietal edge forms a sharp point medially but crushing anterior to this region has obscured its relationships to the rest of the skull. Laterally, and slightly posterior to this anterior tip, a smooth, stout projection buttresses the median portion of the parietal from below. Presumably, from its position, this buttress is formed by the postorbital but the sutures in this area are obliterated by coössification and a large median crack, extending from the parietal to the prefrontal area, further hinders positive identification.

Posteriorly, the parietal thins laterally to form the anterior edge of the frill fenestra. Since none of the edges of these fenestrae are preserved in UA 40, their position can only be estimated. What appears to be an anterior extension of the parietal is preserved on the left side of the skull, lying in a poorly preserved groove on the medial surface of the squamosal. The parietal is tco badly crushed in this area for comparison with NMC 1254b but the groove in the squamosal is broad but shallow, as it is in the comparable region of NMC 1254.

The shape of the supratemporal fossae of UA 40 also must be restored, as lateral crushing has distorted this area. Enough of this region is preserved, however, to indicate that, as in Chasmosaurus and Pentaceratops, the supratemporal fossae of Eoceratops were long and relatively narrow, following the contour of the squamosals, which form the lateral walls of the fossae.

The ventral surface of the frill of UA 40 is very poorly preserved, owing both to crushing and destruction of the bone surface by secondary mineralization. There is a slight concavity beneath the arch of the parietal but the bone here is still much thicker than in any other area of the parietal. Any other features that may have been present on the ventral surface of the parietal have been lost.

Part of the jugal-squamosal suture is preserved in NMC 1254 but the jugal itself is known only from UA 40, where it is a large, complex element, bordering the lateral temporal fenestra and the orbit and forming the external border of the subtemporal fossa. Dorsally, the jugal lies in one plane, with only a slight thickening around the ventral rim of the orbit. Posteriorly, the jugal forms the dorsal and anterior edges of the lateral temporal fenestra. The lateral temporal fenestra of the two specimens of Eoceratops is unique among ceratopsids in that its dorsal border is on the same level as the ventral border of the orbit. In other ceratopsids, the lateral temporal fenestra lies in a relatively more ventral position, although Chasmosaurus brevirostris and Pentaceratops approach the condition seen in Eoceratops. (In psittacosaurids and protoceratopsids, the lateral temporal fenestra is much larger and lies in a much more dorsal position than in any ceratopsid.)

Anteriorly, the ventral edge of the jugal participates in a distinct ridge that continues forward onto the maxillary; posteriorly and ventrally, the jugal is strongly arched, forming a projection that is capped distally by a small, highly rugose epijugal ossification. This jugal-epijugal projection is oriented in a more posterior direction than in other ceratopsids and the bone here is thicker than in the rest of the jugal although the projection is not as strongly developed as in other genera, such as _Pentaceratops_. Medially, the surface of the jugal is smooth and slightly concave, again forming a slight ridge along the rim of the orbit.

The epijugal is incomplete, being damaged ventrally, along with a small portion of the jugal, but its relationships to other elements are clear. The quadratojugal articulates with the posterior edge of the jugal, curving distally to wrap around the ventral edge of the jugal and epijugal. The quadratojugal participates slightly in the rim of the lateral temporal fenestra but most of this edge is formed by the jugal and squamosal. The quadrate is closely applied to the posterior edge of the quadratojugal. On both sides of the skull, the quadrate and quadratojugal have been lost distally but, at least on the left side of the skull, all but the extreme distal parts of these elements are well preserved. The quadrate is visible laterally, posterior to the quadratojugal, although most of the quadrate lies beneath the quadratojugal and the jugal. The quadrate of UA 40 appears to have articulated with the squamosal and exoccipital in the method characteristic of ceratopsids, which was described for NMC 1254, but the ventral surface of the frill is so poorly preserved that it is not possible to describe this area in detail. Distally, the sutures between the quadrate and the quadratojugal and the quadrate and the pterygoid are obliterated by coössification.

The quadrate, quadratojugal and squamosal form the so-called "jugal notch", which in UA 40 is deep and fairly narrow. In UA 40, the anterior, roughened edge of the squamosal projects slightly into this notch but in NMC 1254, this edge is straight.

The pterygoid of UA 40 is a thin, broad element that articulates broadly with the quadrate. The major, dorsal component (quadrate ramus) of the pterygoid is concave posteriorly, curving antero-medially to articulate with the basipterygoid process of the basisphenoid. This articulation, the basal articulation between palate and braincase, is solidly fused in all ceratopsids, with no possibility of intracranial movement at this point. Ventral to the basal articulation there is a strong ridge on the posterior surface of the pterygoid, which continues laterally into the ventral edge of the quadrate ramus of the pterygoid and medially into the corresponding ridge on the opposite side. Ventral to this ridge there is a short, stout process of the pterygoid, which articulates broadly with the postero-dorsal edge of the maxillary. Dorsally, this process shows a broad, trough-like depression in other ceratopsids and probably does so in UA 40 as well but this area is still partially covered with rock matrix. Lateral to this area, articulating with the ventro-lateral surface of the pterygoid and the posterodorsal edge of the maxillary, is a small, rugose, knob-like ectopterygoid. The ectopterygoid-pterygoid suture is obscured by matrix but the ectopterygoid-maxillary suture is visible, although the two elements are firmly fused together.

The maxillary of ceratopsids is a complex element that shows little variation throughout the family. Ventrally, the maxillary of UA 40 is elongate and articulates with the pterygoid, ectopterygoid and premaxillary and bears the only teeth in the upper jaw; dorsally, the maxillary encloses most of the antorbital fenestra and articulates with the jugal, lacrimal, nasal and premaxillary. In UA 40, dorso-ventral crushing has displaced the maxillary somewhat but the relationships of this element are still clear.

The maxillary tooth row in UA 40 can be seen to extend far posteriorly, although the very posterior tip of the maxillary is missing. Anteriorly, the maxillary has a short edentulous portion, the posterior part of which forms a thin, ventral flange. The anterior teeth are lost from the specimen but enough of the tooth row remains to permit a partial description of the dentition of Eoceratops (see below). The maxillary is widest at the approximate center of the tooth row, for while the medial surface of the maxillary lies more or less in one plane, the ventral edge of the lateral surface bulges considerably, presumably to accommodate the curve of the vertical tooth series (see below). On the lateral surface of the maxillary are three fairly large foramina; on the medial surface there is the usual curved row of foramina associated with the teeth of ornithischians (Edmund 1957). The ends of this row lie just dorsal to the tooth row but the central foramina lie further from the teeth.

Dorsally, the maxillary forms part of the anterior edge of the subtemporal fossa. Dorsal to this edge, the ridge found on the jugal continues anteriorly on the maxillary, ending slightly posterior to the maxillary-premaxillary suture, and dorsal to this ridge lies the antorbital fenestra, which, in *Eoceratops* is a very tiny opening. Crushing has partially filled this fenestra in UA 40 and it is not possible to tell if it is a true fenestra or only a fossa, since the medial surface of the maxillary is largely obscured by rock matrix. A short extent of the rim of the antorbital fenestra is formed by the jugal and more dorsally, by the lacrimal.

The lacrimal of UA 40 appears to be a more or less rectangular element, forming a small part of the orbital rim, ventral to the palpebral ossification, but the lacrimal-maxillary and part of the lacrimal-jugal sutures have been obliterated through coössification. This coössification and a large crack, extending from the posterior part of the premaxillary to the palpebral and obscuring the prefrontal-lacrimal suture, make it impossible to define the extent of the lacrimal exactly but from the sutures that are visible, this element appears to be relatively large.

The rostral of UA 40 is missing and the premaxillary is crushed anteriorly but an estimate of at least the posterior extent of the rostral on the premaxillary can be made. The ventral edge of the premaxillary is decurved anteriorly and probably more or less reflects the curve of the ventral edge of the rostral. Further posteriorly is a small ventral flange that probably supported the posterior edge of the rostral. It is not possible to determine the dorsal extent, size or shape of the rostral but based on similarities in the other areas of the skull, this element may have been similar to the rostral of Chasmosaurus.

The premaxillary itself is a large element, articulating posteriorly with the nasal and maxillary and dorsally with the nasal, immediately anterior to the nasal horn core. The posterior articulation with the nasal is complex, with a stout dorsal process of the premaxillary interdigitating with two similar, descending processes of the nasal but the dorsal articulation between these two elements is a relatively simple scarf joint, with a posterior process of the premaxillary overlying the anterior tip of the nasal. The premaxillary forms the anterior and ventral edges of the external narial opening, which is relatively very large and more or less circular in outline except ventrally, where the premaxillary sends a prominent, triangular process into the median portion of the opening. Where the premaxillary and nasal meet on the ventro-posterior border of the external narial opening, there is a rugose thickening, largely composed of the nasal, covering the medial surface of the suture. (The function of this thickening, and of similar features in other genera, is discussed below.) The posterior rim of the premaxillary septum is thickened and anterior to this there is a shallow, circular depression.

Beneath the external narial opening there is a strong ridge that continues the curve of the posterior edge of the opening and passes anteriorly, beneath the triangular flange. Ventrally, the premaxillary forms a partial secondary palate, bounded laterally by prominent ventral flanges, while anteriorly, there is a deep depression in the secondary palate for the reception of the anterior tip of the predentary. The maxillary does not participate in the secondary palate and the vomers, which are extremely thin in ceratopsids (Lull 1933), are not preserved in UA 40.

The occiput of UA 40, although more complete than the ventral surface of the frill, is not well preserved. No trace of the supraoccipital sutures remains, although the exoccipitals can be outlined fairly accurately. As in other ceratopsids, the exoccipitals are broad, wing-like structures that brace the lateral parts of the frill against the occipital condyle. The posttemporal fenestrae are completely closed. There are slight concavities on the postero-ventral surfaces of the exoccipitals and there is a strong depression immediately lateral to the occipital condyle. The condyle itself is a stout, spherical structure supported by a robust peduncle but since all the sutures in this area are obliterated, it is not possible to tell what elements participate in the condyle. Presumably the exoccipitals form most, if not all, of this structure. Dorsal to the condyle, probably in the area occupied by the supraoccipitals, there are two deep, elongate depressions, separated medially by a prominent ridge. Ventral to the condyle, the peduncle of the condyle divides into two ridges that merge into the concave posterior surfaces of the basioccipitals. Again, no sutures are visible in this area. The basioccipitals form large, round basal tubera, the ventral edges of which are thick and rugose. The stout basipterygoid processes are braced against the antero-ventral edges of the basioccipitals and probably much of the anterior surface of the basioccipitals is sheathed by the basisphenoids. Between the basipterygoid processes and dorsal to the pterygoid ridges there is a deep depression, ventral to which there is a short, broad basisphenoid rostrum.

Part of the lateral wall of the braincase is visible in

UA 40, although the area is distorted by crushing. The most prominent feature is a strong arch, formed by the laterosphenoid, that braces the skull roof beneath the posterior edge of the brow horn core. Immediately posterior to the ventral portion of this arch, there is a large but poorly preserved foramen that probably was the exit for the maxillary and mandibular branches of the fifth cranial nerve. On the anterior slope of the arch there are two small foramina that probably represent the exits for the third cranial nerve, dorsally, and the sixth, ventrally. Hay (1909) identified "orbitosphenoid" and "presphenoid" bones in the anterior region of the braincase of Triceratops but in UA 40, although there is an anterior flange of bone in more or less the same area as Hay's "orbitosphenoid" and "presphenoid", separated from the laterosphenoid arch by a short, unossified region, all the sutures are coössified so that the exact nature of this region is uncertain.

Ventrally, much of the palatine of UA 40 has been crushed into the orbit, so that it lies in a more dorsal position than it would have occupied in life. In undistorted skulls, the palatine sends a long dorsal process up to the level of the base of the laterosphenoid arch, bracing both the pterygoid and the vomer (see Hatcher, Marsh and Lull 1907, fig. 24). Ventrally, the palatine has a broad contact with the maxillary, although this area has been distorted by crushing. Behind the palatine there is a deep, V-shaped notch, which probably lies entirely within the pterygoid, as in YPM 1820 (*Triceratops horridus*) (see Hatcher, Marsh and Lull 1907, fig. 24), but the palatine and pterygoid are thoroughly coössified and it is possible that this notch lies between these two elements. Part of the prootic is visible in UA 40, although all the sutures in this region are coössified, but the rest of the lateral wall of the braincase is obscured by crushing and matrix.

Most of the post-cranial skeleton of UA 40 was too poorly preserved to collect (Sternberg 1920) but some additional cranial and postcranial material was retained. This additional material includes fragments from the lower jaw; a predentary; a cervical rib; fragments of the frill and the right brow horn core. The predentary and the cervical rib are similar to comparable elements in other ceratopsids, the brow horn core is identical to that on the left side of the skull and the other material is too fragmentary to be worth describing and is mentioned here only for the sake of completeness.

(c) Revised description of the genus *Eoceratops*

CLASS Reptilia
ORDER Ornithischia
SUBORDER Ceratopsia
FAMILY Ceratopsidae
Eoceratops Lambe 1915
E. canadensis (Lambe 1902)

Referred material - NMC 1254a, a right squamosal; NMC 1254b, a right parietal; NMC 1254c, a right nasal; NMC 1254d, a right prefrontal, frontal and postorbital, coössified; NMC 1254e, a left dentary; NMC 1254, an anterior dorsal or posterior cervical vertebra; all from one individual. UA 40, an almost complete skull with portions of the lower jaws, a cervical rib and an unidentified postcranial fragment.

Horizon and locality - NMC 1254 was discovered by Lambe in 1901, in the Judith River (Belly River) Formation on the east side of the Red Deer River, "a short distance below the mouth of Berry creek", Alberta (Lambe 1915, p.1). UA 40 was discoved by G.F. Sternberg in 1920, in the Judith River (Belly River) Formation on the Red Deer River, on the "east side of Sand Creek about 2 miles south east of mouth of Creek nearly a mile east of Creek" (Sternberg 1920).

Description

Eoceratops is a relatively small, short-faced ceratopsid with close affinities to *Chasmosaurus*, especially *C. kaiseni* and *C. brevirostris*. (Lull (1933, p.96) considered UA 40 to be "a variant, possibly sexual, of *Chasmosaurus kaiseni*" and Sternberg's original field identification of UA 40 was *Chasmosaurus*, as well (Sternberg 1920).) The most characteristic features of the genus *Eoceratops* are the relative shortness and depth of the face; the relatively short but triangular squamosal; the dorsal position of the lateral temporal fenestra and the configuration of the horn cores, the nasal horn core being short, broad and triangular, the brow horn core being relatively long and tapering. UA 40 is an older individual than NMC 1254 but NMC 1254 is somewhat larger and may belong to a different sex or even a different species, but without more specimens it is impossible to gauge the range of variation within the species.

II. Functional craniology

(a) Reconstruction of the musculature

Size, shape, place of attachment, type of attachment and direction of pull of muscles all are important factors in determining the shape of bones (Frost 1964). Therefore, if the analysis of a skeleton is to be more than pure description, it must consider associated musculature as well, not only for an understanding of function but also for an explanation of the shape and surface texture of individual bones. There are several avenues of approach that may be used in reconstructing muscles. Often muscles leave recognizable traces on bone in the form of scars and/or special structures for increasing strength of attachment and in some cases it may be possible to determine type of attachment, direction of pull or other detailed information from such structures (Klaauw 1963). Where several well preserved specimens are available for comparison, muscles may be reconstructed with considerable confidence from such evidence. Where no such clues are available, or where the evidence is ambiguous, consideration of the overall biomechanical requirements of the skeleton may indicate the best choice in a reconstruction. The dangers inherent in such a method are considerable, especially if the reconstruction is to be used for a biomechanical analysis. Used with caution, however, this method is a useful check, and essential where no other evidence is available. Finally, certain higher taxonomic groups show quite detailed similarities in musculature, at least in certain regions (Adams 1919; Edgeworth 1935; Schumacher 1973; Haas 1973; etc.), and one can extrapolate such similarities to extinct members of the same group. (If the similarities are quite extensive among living members and if the fossil member is closely related to living species, such extrapolations may be extremely accurate.)

There are large numbers of artists' conceptions of the life appearance of ceratopsians but there are only four detailed, published reconstructions outlining the entire musculature of particular regions. The first such attempt was Lull's (1908) article on the cranial musculature of Triceratops. In a very thorough analysis, Lull reconstructed both cranial and cervical muscles for a generalized Triceratops, based on YPM 1823 and AMNH 970 (T. serratus) and YPM 1822 (T. prorsus), using the chameleon for comparison with modern reptiles. The next reconstruction of ceratopsian musculature was published in 1935, when L. S. Russell restored the major muscles for the entire skeleton of Chasmosaurus belli, with a view to reconstructing the life appearance of that species. (Russell did not mention which specimens of C. belli he used but two complete skeletons (NMC 2245 and NMC 2280) were described prior to 1935, and presumably these formed the basis of his reconstruction.) In addition, Russell made comparisons with

Sphenodon, a raven and an alligator, although the last was used for the pelvic musculature only. Russell's paper is the only published description of the entire body musculature of a ceratopsian.

In both these reconstructions, the terminology and the basic pattern of the cranial muscles is mammalian. Hence, in 1955, Haas re-analysed the jaw musculature of ceratopsians, including psittacosaurids, protoceratopsids and ceratopsids, using the sauropsid pattern outlined by Lakjer in 1926 (see Säve-Söderbergh 1945). This article was followed by Ostrom's (1964*a*) reconstruction of the cranial musculature of *Triceratops*, based on four different species and also using Lakjer's pattern and terminology.

Not all workers use Lakjer's scheme. Iordansky (1970) felt that the nomenclature of the portions of the *M. adductor mandibulae externus* should be specific for each group of sauropsids, because the variation within the Sauropsida is so great. Nonetheless, modern anatomists use Lakjer's scheme extensively (see Schumacher 1973; Haas 1955, 1963, 1973; Ostrom 1961, 1962, 1964*a*; Säve-Söderberg 1945; and others) and extreme modifications can be described as well by their deviations from Lakjer's basic pattern as by the establishment of a new one. Further, Säve-Söderberg (1945) considered the mammalian *M. temporalis* to be homologous with only a part of the sauropsid *M. adductor mandibulae externus*. Some anatomists do not share this view (for example, Romer 1970) but since the exact homology is uncertain, the term "*temporalis*" is restricted here to the mammalian jaw adductor and in discussing ceratopsian cranial muscles, the present work employs Lakjer's classification of trigeminal muscles, as outlined by Säve-Söderberg (1945), Schumacher (1973) and Haas (1973).

Modern classifications of visceral muscles are based on early studies of selachians (Schumacher 1973). In selachians, the trigeminal muscles form a levator for the upper jaw, a dorsal constrictor, which closes the mouth, and a ventral constrictor, which raises the floor of the mouth. In sauropsids, the trigeminally innervated levator and dorsal constrictor combine to form two muscle masses: the adductor mandibulae group, the main adductors of the lower jaw, and the smaller, more medial constrictor internus dorsalis group (Webster and Webster 1974). The ventral constrictor associated with the mandibular arch in sauropsids forms the *M. constrictor ventralis trigemini* (Webster and Webster 1974).

In 1914, Luther classified the trigeminal adductor muscles of amphibians according to their relationship to the branches of the fifth cranial nerve and in 1926, Lakjer extended this classification to the Sauropsida (Säve-Söderberg 1945). Lakjer divided the sauropsid *M. adductor mandibulae* into *externus*, *internus* and *posterior* portions, the *pars externus* lying lateral to the maxillary and mandibular branches of the trigeminal nerve, the *pars internus* lying anterior or medial to the maxillary, but lateral to the ophthalmic branch, and the *pars posterior* lying posterior or medial to the mandibular branch (Säve-Söderberg 1945). The constrictor internus dorsalis group also can be classified in this way, as it generally lies anterior and medial to the ophthalmic branch, but the relative positions of the members of this group are somewhat variable, whereas the divisions of the adductor mandibulae group are remarkably constant considering the variation within the Sauropsida (Säve-Söderberg 1945).

The *M. depressor mandibulae* is a facial muscle, representing the combined levator and dorsal constrictor of the hyoid arch (Webster and Webster 1974). Nonetheless, since the *M. depressor mandibulae* opposes the action of the jaw adductors, opening the mouth, it is appropriate to discuss it in connection with the trigeminal muscles.

The *M. adductor mandibulae* generally is the largest and most complex of the sauropsid adductor muscles. According to Haas (1955, p.12), this muscle is also "the most inconstant element of the whole group of trigeminus muscles". Generally, the *M. adductor mandibulae externus* consists of a *pars superficialis*, inserting anteriorly and superficially on the lower jaw, and a *pars medialis* and *pars profundus*, separated by a basal aponeurosis ("Bodenaponeurosis" or "external tendon"), inserting onto the dorsal margin of the mandible, or on the coronoid process, where that structure is present (Haas 1973). Such a subdivision is not possible in all cases. Snakes, for instance, usually lack a

Bodenaponeurosis (Haas 1973) and the relationships of the adductor mandibulae tendons of crocodilians require a different scheme (Schumacher 1973). Where a Bodenaponeurosis is present, the *M. adductor mandibulae externus medialis* inserts on its lateral face and the *pars profundus* on its medial face (Haas 1973).

In most modern diapsids, the *M. adductor mandibulae externus superficialis* arises from the medial surface of the upper temporal arch (Haas 1955). In *Sphenodon* (see Haas 1973, fig. 7), this muscle arises from the postorbital bar and Haas (1955, p.13) reconstructed the origin of the *pars superficialis* of *Protoceratops* on "the medial side of the upper temporal arch ... and probably from the postorbital bar as well." (Ostrom (1964*a*, p.18) placed the origin of the *pars superficialis* of *Triceratops* "on the medial surface of the upper temporal arch.")

In *Eoceratops*, as shown by both UA 40 and NMC 1254a, there is, potentially, considerably more room for the origin of the *pars superficialis* than there is in *Protoceratops*. The upper temporal arch is much deeper and the lateral temporal fenestra is correspondingly much smaller, while the area posterior to the orbit is much wider. Since, in neither specimen of *Eoceratops* does the medial surface of the upper temporal arch or of the postorbital area show muscle scars or special structures for muscle attachment, it is not possible to determine the area of origin directly. It is possible that the *pars superficialis* was much more extensive in ceratopsids than in *Protoceratops* and that its origin spread out over the medial surfaces of the squamosal, jugal and postorbital, but there is no evidence of such an attachment in *Eoceratops*. On the other hand, the edges of the lateral temporal fenestra show scars indicating tendinous muscle attachments and it is difficult to explain the presence of these small fenestrae if they did not serve in some way for muscle attachment.

Haas (1955) felt that the decrease in size of the lateral temporal fenestra in ceratopsids was correlated with a reduction in bulk of the *pars superficialis* with respect to *Protoceratops*. Certainly there is no evidence to indicate that this was not the case in *Eoceratops*, though despite the relative reduction, this still would have been a fairly powerful muscle. (The area of insertion (see below) shows striations indicating a strong, tendinous attachment and the area around the lateral temporal fenestra, and on the medial surface of the fascia that presumably covered that fenestra, would provide sufficient area of attachment for a relatively large muscle.) The lateral temporal fenestra of ceratopsids is too small to allow a significant degree of lateral bulging, however, even if the *pars superficialis* were a relatively small muscle, so while the fenestra probably functioned in this manner in *Protoceratops*, it is unlikely that it did so in *Eoceratops*.

In *Sphenodon*, most of the *pars superficialis* inserts on the dorsolateral surface of the coronoid process and on the lateral surface of the large Bodenaponeurosis (Haas 1973) and Haas (1955) and Ostrom (1964a) reconstructed basically similar insertions for *Protoceratops* and *Triceratops*. The coronoid process in *Eoceratops*, as in all ceratopsids, is relatively much higher and more narrow than in *Protoceratops*, with a distinct anterior hook that is absent in the Protoceratopsidae. Well preserved specimens of ceratopsids show distinct parallel striations on the dorsolateral surface of the coronoid process and anterior hook and on the lateral surface of the most dorsal portion of the coronoid process there is a flat surface, sloping medially at its dorsal edge. In NMC 1254e, this surface is surrounded by striations but is itself too poorly preserved to show either the presence or absence of similar striations. The dentary of UA 40 is not preserved as well as NMC 1254e but the flat surface is distinct and striations are visible posteriorly, along its ventral edge. This surface and the surrounding striations represent the insertion of the *pars superficialis*, although part of this insertion probably involved the lateral surface of the Bodenaponeurosis as well, as in *Sphenodon*. (Lower jaw elements other than the dentary and predentary are not preserved in either specimen of *Eoceratops canadensis*, but comparisons with other specimens, for example, ROM 4519 (*Centrosaurus apertus*), indicate that part of the insertion may have been on the surangular as well.)

Tendinous attachments tend to leave rugosities on the surface of the underlying bone, while fleshy attachments leave relatively smooth surfaces (Olson 1971). The characteristic pattern described for *Eoceratops* thus may be interpreted as a largely, if not wholly, tendinous insertion and the deep anterodorsal striations may indicate an area of dense fascia where the epimysium of the *pars superficialis* merged with the lateral surface of the Bodenaponeurosis. According to Frost (1972, p.166): "fibrous tissue in bulk possesses some mechanism which brings most of its individual fiber bundles into alignment parallel with the tension loads it carries, thereby promoting maximum tensile strength with a minimum amount of collagen." An arrangement in which the striations on the surface of the bone, as well as the tendinous fibers of the muscle attachment, were parallel to the tension loads created by contraction of the *pars superficialis* would increase tensile strength further,[1] hence the supposition that the direction of the striations indicates the direction of pull of the muscle, at least at the area of insertion. From the lateral surface of the coronoid process, the *pars superficialis* passed dorsally and somewhat posteriorly to attach around the lateral temporal fenestra and on the associated fascia. Although, using the striations on the coronoid process, one can define the limits of the insertional area fairly precisely, no such estimate is possible for the area of origin, as this muscle may have been pinnate, converging on the coronoid process, so that the area of origin was larger than the area of insertion.

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[1] "In osteogenic tissue subjected to pressure and tension, osteoblasts and osteogenic fibers become oriented along the lines of stress" (Le Gros Clark 1971, p.105). Such an arrangement provides great rigidity and strength for resisting tension loads paralleling the long axis of the fibres (Frost 1972).

Haas (1955) reconstructed a separate, lateral portion of the pars superficialis of Protoceratops. Although the area of insertion of the pars superficialis in Eoceratops, and other ceratopsids, is large, relatively it occupies a much smaller portion of the coronoid process than does the equivalent area in Protoceratops. In Protoceratops, "a conspicuous horizontal crest through the surangular and adjacent posterior parts of the dentary indicates the outermost ventral border of the attachment" of the pars superficialis (Haas 1955, p.15). The surface above this crest faces dorsally, toward the area of origin of the pars superficialis, while the area below the crest slopes in such a way that the pars superficialis could not attach to it without bending over and around the crest (Haas 1955). Haas (1955, p.15) derives the pars superficialis lateralis "from the lower face of the lower temporal arch", a radical departure from the condition seen in modern sauropsids. This lateral portion would have inserted on the surangular crest and the concave area dorsal to the crest. The ventral surfaces of the jugal and quadratojugal of Protoceratops are excavated and this excavation faces the surangular crest in such a way that a pars superficialis lateralis arising there would have had "excellent pulling power" (Haas 1955, p.16). In Psittacosaurus mongoliensis there is also a trough on the ventral surfaces of the jugal and quadratojugal, facing a similar caudolateral crest on the mandible (Haas 1955). According to Haas (1955, p.16):

> "Such a muscle would explain the presence of the strange angulation of the lower temporal arch with the accessory epijugal at the top. The width of the ventral concavity of the arch points to the possibility of a very substantial muscular attachment. Such a muscle could have become differentiated from a normally situated superficialis by an extension of the orthodox origo at the upper arch onto the fascia covering the lower temporal fenestra, until the lowermost fibres reached the under side of the lower arch. Probably a stage of general enlargement of the origo area preceeded the splitting into two separate bellies."

Haas (1955, p.16) noted that there is a similar jugal-quadratojugal "angulation" in Protoceratops, but the angle of the jugal-quadratojugal area is on a level with the jaw articulation, causing a reduction of the angle "and a caudal rotation of the epijugal which, instead of being located in front of the lower end of the quadrate, bulges considerably beyond the level of the mandibular joint". (It should be noted that Gregory interpreted the jugal "horn" in Psittacosaurus as an area of attachment for a highly developed masseter muscle (Osborn 1924) but did not expand upon this idea, at least in print.)

In all ceratopsids there is a dentary-surangular ridge, more or less at the base of the coronoid process, but unlike the ridge in Protoceratops, this structure often is not defined sharply, and it never forms the base of a dorsally-facing concavity. Also, the epijugal projection lies even farther posterior to the level of the jaw articulation than in protoceratopsids and there is no deep ventral excavation of the jugal and quadratojugal, these elements being essentially vertical in orientation. Thus, not only is there no clear indication of an area of origin for a separate lateral portion, but the extreme posterior position of the jugal-epijugal projection would force such a muscle to pull in an essentially posterior direction, an unlikely action for a jaw adductor. Thus there is no evidence of a *pars superficialis lateralis* in the Ceratopsidae, although Haas' evidence for such a muscle in the Psittacosauridae and Protoceratopsidae is convincing.

In some modern reptiles (*Sphenodon*, lizards, some snakes (Haas 1973)), the most anterior and superficial fibres of the *M. adductor mandibulae externus* form a separate *M. levator anguli oris* and/or *M. retractor anguli oris*, attached to the corner of the mouth. This muscle may be single, as in the vast majority of lizards, or clearly double, as in *Sphenodon* (Haas 1973). In most cases, where the *M. levator anguli oris* (and/or the *M. retractor anguli oris*) is present in modern reptiles, it arises from the ventral surface of the upper temporal arch (Haas 1973). The only exceptions are certain snakes (these muscles are not present in all ophidians), where the upper temporal arch is missing and the *M. levator anguli oris* arises from the antero-lateral rim of the open temporal area (see illustrations in Haas 1973).

Neither Haas (1955) nor Ostrom (1964*a*) mentioned a *M. levator anguli oris* in their reconstructions, although Haas (1969) reconstructed one for ankylosaurs, but Galton (1973) suggested that the *M. levator anguli oris*, or the *M. adductor mandibulae externus superficialis* (*sensu stricto*), formed a lateral cheek in almost all ornithischians. Lull (1903, 1905, 1908, 1933 and in Hatcher, Marsh and Lull 1907), L. S. Russell (1935) and Sternberg (1951) all presumed that cheeks were present in ceratopsians, mainly to prevent masticated food from falling out of the mouth. Unfortunately, Lull's (1908) and L. S. Russell's (1935) restorations labelled this cheek the "*M. buccinatorius*". Brown and Schlaikjer (1940*c*) objected to this designation, noting that the *M. buccinatorius* is a facial muscle peculiar to mammals and that it is derived from the *M. sphinctor colli*, which in reptiles lies on the side of the neck. Haas (1955, p.2) objected to the reconstruction of cheeks in ceratopsians on the basis that "no [modern] sauropsid with cheeks is known" and as well criticised the use of a mammalian *M. buccinatorius*. The prejudice created by the early use of a mammalian cheek muscle is unfortunate because neither the arguments of Brown and Schlaikjer (1940*c*) nor of Haas (1955) refute Lull's (1903) assertion that cheeks neccessarily were associated with the ceratopsian dentition to prevent loss of food during mastication. While it is true that no living sauropsids have cheeks, despite the fact that several reptilian species are at least partially herbivorous, no modern reptile masticates its food to the degree suggested by the ceratopsian dentition and jaw structure (Bellairs 1970). There are lizards, such as *Uromastix* and some chameleons, that chew their food and some lizards crush or shear both animal and plant material (Robinson 1967). According to Bellairs (1970, p.159), however, "little is known ... about the jaw movements of herbivorous present-day reptiles, and it is uncertain whether they can exert grinding pressures like the jaws of certain extinct forms, and of herbivorous mammals." Therefore, it does not follow neccessarily that since modern sauropsids lack cheeks, the same must have held true for ceratopsians.

With the exception of a few primitive genera, ornithischians possess heavy, conspicuous ridges above the maxillary tooth row and below the dentary tooth row (Galton 1973). Haas (1955) suggested that these ridges supported large glands and emphatically denied the possibility that these structures were sites of attachment for a muscular cheek but since a cheek is indispensible for prolonged mastication and since the ridges occur in precisely the areas where such a cheek would attach, it seems unneccessary to postulate the existence of glands for which no other evidence is available.

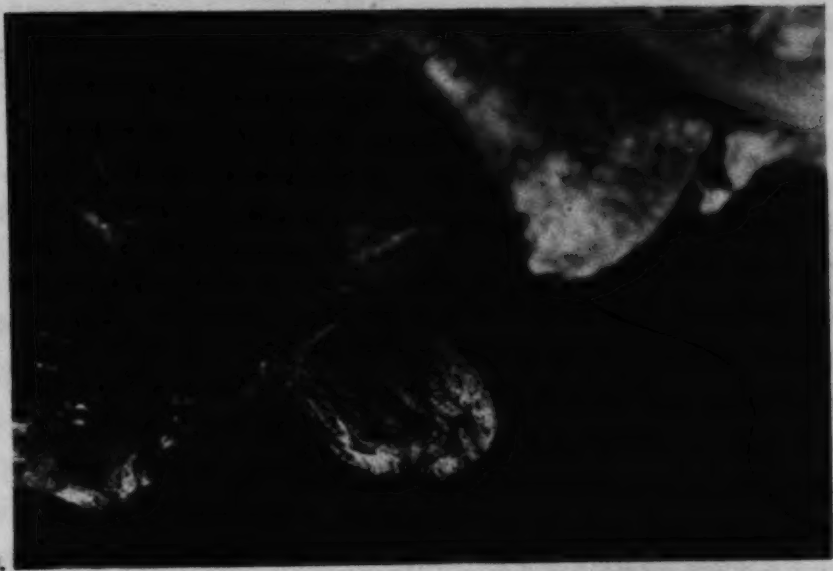
Galton (1973) felt that the cheeks of ornithischians would not have been in close proximity to the teeth and could not have been used to re-position food so that connective tissue and skin would serve as well as contractile muscle. Alternatively, Galton felt that the cheeks may have been muscular in some ornithischians but not in others (Galton 1973). At least in ceratopsians, it seems that a lateral cheek could have approached the teeth closely. Anteriorly, the dentary ridge and the dentary tooth row converge so that a thick, muscular cheek would lie adjacent to the teeth. The hyoid apparatus of ceratopsians is well developed (Lull 1933; Colbert 1945) and presumably supported a well developed tongue that could function to re-position food during mastication. Nonetheless, it is possible that the cheek was at least partially muscular and also functioned in this respect.

In Eoceratops, the maxillary ridge is not preserved in NMC 1254 but is distinct in UA 40, continuing the curve of the ventral edge of the jugal and fading into the general bone surface above the anterior portion of the maxillary tooth row. The ridge has its maximum lateral thickness below the antorbital fenestra, where it forms a low, rounded lateral keel that presumably marks the upper limits of the insertion of the cheek muscle. Other than this keel, the surface of the maxillary ridge is smooth. UA 40 and NMC 1254e are similar with respect to the dentary ridge. This ridge continues the anterior curve of the coronoid process, fading into the general bone surface near the anterior part of the tooth row, then re-appearing as a broad low ridge that passes dorsally into the posterior edge of the articular surface receiving the predentary. The dentary ridge is much less conspicuous than the maxillary ridge and more or less parallel to the tooth row, at least posteriorly, whereas the maxillary ridge is distinctly curved.

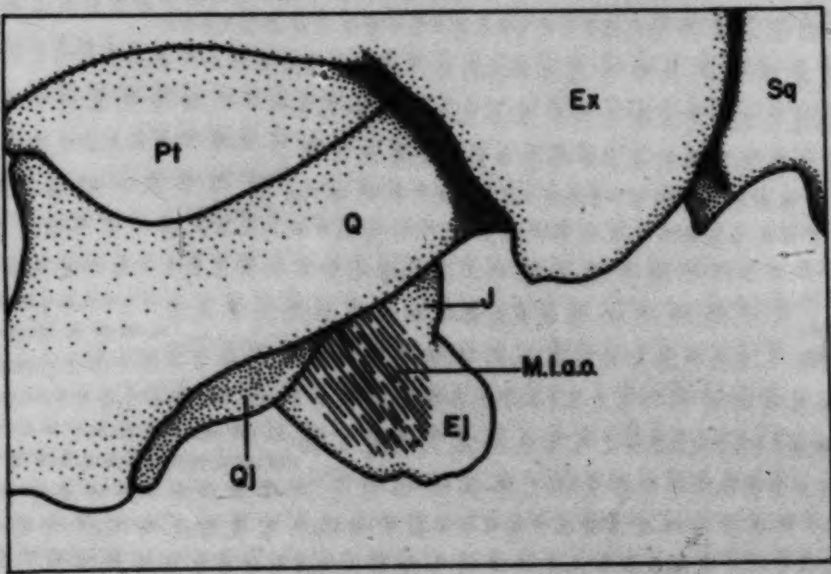
Lull (1908), L. S. Russell (1935) and Galton (1973) reconstructed the cheeks reaching to the level of the anterior end of the tooth row, with a horny beak sheathing the more anterior ends of the jaws. Since the maxillary and dentary ridges are restricted to the area of the tooth rows, and cheeks would be neccessary along the tooth rows but not anterior to them, this reconstruction is retained here. As Lull (1905, p.422) has pointed out, "in herbivorous mammals the gape only includes the prehensile and never the masticatory portion" of the jaw, so it seems reasonable to postulate a similar gape in ceratopsians.

Both Lull (1908) and L. S. Russell (1935) restored the cheek muscle with vertically oriented fibres, but Galton (1973, p.83) felt that the muscle was pinnate, as in many mammals, "with fibres passing obliquely backwards from the maxilla and dentary to the body of the cheek." In a specimen of Centrosaurus sp. mounted at the University of Alberta (UA 11735), the ventro-medial surface of both jugals shows distinct, parallel striations, oriented in an antero-dorsal to postero-ventral direction (Fig. 12). (The medial surface

Fig. 12. Medial surface of the jugal of UA 11735 (*Centrosaurus* sp.) showing scars marking the site of attachment of the *M. levator anguli oris*.



a.


Pt
Q
Ex
Sq
J
M.l.a.o.
Ej
Qj

b.

of the jugal of UA 40 is not well enough preserved to show such scars.) The unfavourable orientation of a *pars superficialis* (*sensu stricto*) passing from this position to the lower jaw indicates that some other muscle arose here. Such a position would be extremely advantageous for the origin of a pinnate cheek muscle, here interpreted as the *M. levator anguli oris*. (Birds and crocodilians, the closest living relatives of the ceratopsians, lack a *M. levator anguli oris* (Haas 1973) but this condition may represent a secondary loss in forms with feeding mechanisms entirely unlike those of ceratopsians.) The deep striations on the jugal indicate a strong tendinous insertion, presumably with muscle fibres diverging obliquely from it to insert on the dentary and maxillary ridges.

Galton (1973) felt that there may have been a longitudinal *M. retractor anguli oris* as well, but with a strong tendon gathering the fibres of the cheek muscle, this muscle itself would have had a certain retraction component and a separate *M. retractor anguli oris* may not have been neccessary.

It is profitable to discuss the *medialis* and *profundus* portions of the *M. adductor mandibulae externus* together, since the restoration of these two muscles is important in interpreting the function of the ceratopsian frill.

In modern sauropsids, the *pars medialis* and *pars profundus* of the *M. adductor mandibulae externus* generally fill most of the upper temporal fenestra (Haas 1973). The *M.*

pseudotemporalis also may be involved (Haas 1973) but, as described below, the M. pseudotemporalis of ceratopsians occupied an extreme anterior position, precluding any entry into the upper temporal fenestra. Haas (1955, p.17) stated that, in Protoceratops, "the adductores externi medialis and profundus occupied, as in other reptiles with a wide upper temporal window, the large osseus frame of the frill" and Lull (1908), L. S. Russell (1935) and Ostrom (1964a) also restored the major jaw adductors at least partially covering the dorsal surface of the frill. Among lizards, chameleons have the largest upper temporal fenestrae (Haas 1973) and they also approach ceratopsians more closely than any other modern sauropsid in the development of a cranial crest or frill. In these forms (see illustrations in Haas 1973) the dorsal surface of the frill is covered with the pars medialis and pars profundus, but a similar condition may not have existed in ceratopsians.

According to Haas (1955, p.17):

> "the depression at the posterior half of the frontals indicates the anterior border of what was probably a bulging muscle mass which filled the whole frame of the frill.... Along the posterodorsal frame of the frill a distinct borderline marking the attachment of the fanwise diverging muscle mass is clearly distinguishable; this line parallels exactly the posterior margin of the frill.... The lateral frame of the frill formed by the postorbital and the squamosal, has a rather sharp margin, which probably supported a tough aponeurosis extending across the whole enlarged upper temporal fossa."

In making his reconstruction cf Protoceratops, Haas (1955, p.3) admitted that he used "a rather limited number of medium-sized and large specimens (A.M.N.H. Nos. 6408, 6414, 6431), being guided by an intention to choose the most completely preserved specimens with their own mandibulae", and he made no attempt to analyse possible age- and sex-related variations. According to Kurzanov (1972), however, ontogenetic changes in _Protoceratops_ do affect some of Haas' conclusions. Kurzanov (1972, p.94) stated that Haas' reconstruction would be possible

> "only in very young animals, when the frill was relatively low and narrow. With increasing age the margins of the frill were increasingly deflected sideways and slightly downward. Therefore, the lateral part of the medial fascia [of the external adductor] would inescapably have to have bent practically at a right angle in adult animals in order to pass across the superior temporal fossa. This is highly improbable. Even if it is assumed that there was a separate lateral fascia alongside the medial fascia, it also would have had to function at an angle of 90°, practically without affording any assistance to the main muscle mass."

Therefore, Kurzanov reconstructed the medial fascia of the _M. adductor mandibulae_ arising at the base of the frill, from crests on the inner surface of the exoccipitals (see Brown and Schlaikjer 1940_c_, fig. 8A). In this position, even if the frill were perpendicular to the skull, as it is in some adult individuals (Kurzanov 1972), there would be no inflection of the muscle mass. Thus, the faint "sigmoid line" crossing "the upper temporal fenestra in front of the anterior border of the wide perforation of the parietal" (Haas 1955, p.18) represents the most posterior limit of the entire _M. adductor mandibulae_ and not, as Haas supposed, the division between the _pars medialis_ and _pars profundus_. (The significance of the other structures mentioned by Haas in connection with the origin of the *M. adductor mandibulae* will be discussed in a later section.)

For ceratopsids, as well as for *Protoceratops*, most authors reconstruct the major jaw adductors covering the dorsal surface of the frill. Haas (1955, pp.18-19) stated that instead of the

> "slight, ridge-like prominence dividing the two muscular areas in *Protoceratops*, a freely jutting bony lamella is developed in *Monoclonius* [and *Centrosaurus*] and *Styracosaurus*, certainly the base for a tough fascia which ossified gradually as it approached the area of attachment at the parietal. In this particular case, however, both muscles took part in over-roofing and covering the perforation of the frill. This is shown quite convincingly by the posterior continuation of the accessory bone blade, which terminates at the posterodorsal end of the fenestration of the frill."

Ostrom (1964*a*, p.12) also concluded that "for most ceratopsians, surface topography and patterns suggest that the frill was almost entirely covered by large muscle sheets", although for *Triceratops* he restricted the muscles to "the immediate vicinity of the supratemporal fenestra." Ostrom (1964*a*, pp.12-13) also stated, however: "it is quite possible that a deeper pars profundus of the M. adductor externus was attached by a strong fleshy origin about the borders of the supratemporal fenestra, leaving a distinct scar of origin. This would account for the features preserved in nearly all *Triceratops* frills. A longer pars medialis of the M. adductor externus may have attached by a thin sheet of fascia to the frill margins and left little or no indication of its attachment."

Lull (1908) reconstructed the "*M. temporalis*" of *Triceratops* arising from the supratemporal fenestra, although neither his description nor his illustration (1908, pl. I) indicates the posterior extent of this muscle. In 1903, however, Lull stated that the posterior portion of the squamosal of AMNH 970 (*T. serratus*) showed muscle scars, indicating that he too, believed that at least a large portion of the dorsal frill surface was covered by muscle.

L. S. Russell (1935, p.41) placed the "*M. temporalis*" on the dorsal surface of the frill in all ceratopsians, stating that

> "in *Protoceratops*, ... it [the "*M. temporalis*"] was a broad, fan-like sheet, covering almost the entire parietal portion of the crest, passing forward through the supratemporal opening, and attaching to the inner side of the coronoid process. The backward extension of the crest in *Chasmosaurus* ... greatly lengthened this muscle, with corresponding increase in contractile power, but there was no essential change from the condition in *Prctoceratops*. *Styracosaurus* ... and *Centrosaurus* ... have the origin area more restricted, owing to the smaller size of the crest and its fenestrae. The area of the muscle is clearly defined in *Styracosaurus*; on the medial side there is an unobstructed channel from fenestra to supratemporal opening, but more laterally the muscle is cut off abruptly along a transverse line. Similar conditions appear in *Centrosaurus* and the somewhat later *Anchiceratops* ... , but here the posterior portion of the muscle appears to have been thin and membranous. Finally, in *Triceratops* ... , the sharp line of origin first seen in *Styracosaurus* has become the posterior margin of the supratemporal opening, indicating that the temporalis muscle was restricted to that vacuity".

Russell concluded that the enlarged crest of ceratopsids developed in order to increase the size and area of attachment of the "*M. temporalis*", with the frill fenestrae providing room for this muscle to expand.

Kurzanov's (1972) analysis showed that such a condition was unlikely for *Protoceratops* but no one has questioned similar reconstructions for ceratopsids.

All members of the Ceratopsidae have greatly expanded frills, variously ornamented, and all genera except *Triceratops* have a pair of large fenestrae in the frill, separate from the supratemporal fenestrae. (Some specimens show supernumerary fenestrae, the significance of which is discussed in a later section, but the presence of such fenestrae does not affect the following discussion.) In *Triceratops*, the region occupied by a fenestra in other ceratopsids is extremely thin and probably represents the secondary closure of a fenestra. The surface of the bone forming the floor of the supratemporal fossa, in all ceratopsids, is smooth, although generally it shows broad, irregularly-spaced undulations.

Many writers mention the presence of vascular grooves on the ceratopsian crest but there is little uniformity in such descriptions. Some workers (for example, Lull 1933; Brown 1933) have used the degree of vascularization as a taxonomic character while others (Gilmore 1931; Hatcher 1905; Lambe 1913) have stated that vascularized frill surfaces are the usual condition in ceratopsids. In some specimens, such as ROM 5436 (*Chasmosaurus brevirostris*) and

ROM 4519 (Centrosaurus apertus), the dorsal and ventral surfaces of the frill are smooth; in others, such as ROM 5135 (Arrhinoceratops brachyops) and AMNH 5351 (Centrosaurus nasicornus), the dorsal surface is more heavily vascularized than the ventral and in others, such as AMNH 5251 (Anchiceratops ornatus), the degree of vascularization is roughly similar on both surfaces. (Sometimes, as in AMNH 5402 (Chasmosaurus belli), the dorsal surface of the median parietal bar is vascularized while the dorsal surface of the squamosal is smooth.)

There may be some degree of taxonomic significance in the development of vascularized surfaces on the frill of ceratopsids but the basic tendency towards vascularization is widespread and even within one genus there may be considerable variation in this character. Lull (1933) stated that Chasmosaurus posesses vascular marks on the dorsal surface of the parietal, but not on the squamosal, a character supposedly shared with Torosaurus. While this description holds true for some specimens of Chasmosaurus (AMNH 5402 (C. belli) (pers. obs.) and AMNH 5656 (C. sp.) (Lull 1933)), in YPM 2016 (C. belli) and NMC 2280 (C. belli), the dorsal surface of both the parietal and the squamosal is vascularized and in ROM 5436 (C. brevirostris) and AMNH 5401 (C. kaiseni), both dorsal and ventral surfaces of the frill are smooth.

Lull (1933) also felt that the "long-crested" genera, such as Chasmosaurus, Pentaceratops, Arrhinoceratops and

Anchiceratops had less heavily vascularized frills than the "short-crested" genera (Monoclonius, Centrosaurus, Brachyceratops, Styracosaurus, and Triceratops, according to Lull's definition). In this respect, Lull (1933) felt that Anchiceratops, which has deep vascular impressions, was anomalous. Anchiceratops is not the only "long-crested" ceratopsid with a deeply vascularized crest, however, for the same condition is seen in Arrhinoceratops, and Pentaceratops shows distinct vascular marks, at least on the dorsal surface of the frill. In ROM 4519 (Centrosaurus apertus), on the other hand, the dorsal surface of the frill is smooth, so one cannot say that all "short-crested" genera are characterized by heavily vascularized frills.

Degree of vascularization could be related to age, as Hatcher (1905) suggested for YPM 1834 (Triceratops brevicornus), which has a highly vascularized frill that Hatcher interpreted as an indication of advanced age, but in YPM 1821 (T. flabellatus), a young individual with open sutures, portions of the dorsal surface of the frill show deep vascular markings. If this feature is age-related, its distribution, even between species of the same genus, is not sufficiently stable to be used as a taxonomic character.

State of preservation and individual variation probably affect the observable amount of vascularization as well, so that the use of these markings in ceratopsian taxonomy is ill-advised. In all cases where such markings are present, however, they end abruptly at the edge of the supratemporal fossa, the edge of which is separated distinctly from the rest of the dorsal surface of the frill by a low ridge (Fig. 13). Between the ridge and the anterior edge of the frill fenestra, there is almost always an area of vascular markings, although sometimes these are faint or poorly preserved due to the delicate nature of the bone in this area. (In Triceratops, which lacks the normal frill fenestrae, the vascular markings persist to the edge of the supratemporal fenestra.) Even in those cases where the dorsal surface of the frill lacks vascular markings, there is a low ridge separating the supratemporal fossa from the rest of the frill. This ridge, and the dramatic change in surface texture in those specimens showing vascular markings, indicate the most posterior limit of the M. adductor mandibulae. (Note that Sternberg (1940) made a similar assumption for Chasmosaurus.)

As mentioned above, fleshy muscle attachments, especially if they are large, tend to leave smooth scars on bone. Usually, such an area of attachment is surrounded "by faint ridges caused by the attachment to the periosteum of the intermuscular fibrous septa between which the muscle lies" (Le Gros Clark 1971, p.79). Although such ridges may occur between two fleshy insertions, the area posterior to the ridges described above for ceratopsids does not exhibit the characteristics one would expect of a fleshy attachment. Specimens exhibiting vascular markings on the frill could not have had fleshy attachments overlying these bony

Fig. 13. Left supratemporal fossa of UA 11735 (*Centrosaurus* sp.) showing abrupt change in surface texture marking the most posterior limit of muscle attachment on the dorsal surface of the frill. Below, left lateral view of UA 11735, with area shown in detail above outlined in black.

grooves, for the muscle would have produced a broad, flat area, lacking vascular markings, as did the muscle in the supratemporal fossa. In those specimens lacking such vascular grooves, one might postulate a fleshy origin from the smooth bone surface but the degree of vascularization is not distributed systematically among ceratopsids and one would not expect a character as important as the origin of the most powerful jaw adductor to be variable to such a great extent between "vascularized" and "non-vascularized" forms. Further, there are no structures on the posterior part of the frill, such as smooth, broad, concave areas or slight ridges, to suggest the presence of such fleshy attachments. The "freely jutting bony lamella" mentioned by Haas (1955, pp.18-19) in "*Monoclonius*" (*i.e.*, *Centrosaurus*) and *Styracosaurus* does provide part of the area of origin for the *M. adductor mandibulae* (see below). The "posterior continuation of the accessory bony blade", however, which Haas (1955, p.19) felt "marks [the] origin of [the] covering aponeurosis for [the] deep frill muscle" is present only in AMNH 5239 (*Centrosaurus flexus*). In neither ROM 4519 (*Centrosaurus apertus*) nor UA 11735 (*Centrosaurus* sp.), both of which have extremely well preserved frills, does such a ridge appear, nor is it present in *Styracosaurus* (see Lull 1933, pl. VIIIA and B). In AMNH 5239, this ridge is not accompanied by any change in surface texture, being surrounded by vascular grooves, nor does a similar ridge appear on the right side of this skull. (There is a ridge on the right side of the median parietal bar but it has an entirely different shape and a completely different position. Both ridges appear to be caused by crushing rather than by muscular attachment.) Haas (1955, fig. 11) reconstructed the "probable border of [the] superficial portion of frill muscle" of Styracosaurus on the dorsal surface of the median parietal bar and near the edges of the frill fenestra. The most complete and well preserved skull of Styracosaurus (NMC 344 (S. albertensis), see Lull 1933, pl. VIIIA and B) shows no ridge, indentation, change in surface texture or other scar or special structure in these areas to indicate a muscular attachment. As in other ceratopsids, there is a smooth floor in the supratemporal fossa of NMC 344, separated from the rest of the dorsal surface of the frill (which, in this case, is highly vascularized) by a distinct low ridge (see Lull 1933, pl. VIIIB).

Thus, it seems highly improbable that a fleshy muscle existed posterior to the supratemporal fenestra of ceratopsids. Ostrom (1964a) and L. S. Russell (1935) have suggested that in some genera, at least part of the adductor muscle may have been a long tendon that covered the dorsal surface of the frill to the posterior margin. Since tendons act to concentrate muscle attachments in relatively restricted areas, it is unlikely that a tendon would have attached to the entire dorsal surface of the frill and no striations or other attachment structures associated with tendons indicate such an origin. If, on the other hand, a broad tendon lay over the surface of the frill and attached only to its posterior edge, it would obliterate the vascular marks. Soft tissues, even muscles at rest, tend to limit the growth of adjacent bones and result in flattened surfaces on those bones (Murray 1936; Le Gros Clark 1971). Vascular grooves in the surface of bone are produced in this manner, by the pressure caused by the blood vessels, and "it may be supposed that the local pressure on the vascular periosteum disturbs the blood supply to the underlying bone, leading to a loss of vitality and subsequent absorption" (Le Gros Clark 1971, p.79). If a tendon overlay such vessels, its pressure against the surface of the bone also would tend to flatten the bone surface, and thus obliterate vascular grooves.

Since neither muscle nor tendon seems to have occupied the dorsal surface of ceratopsid frills, it is likely that the skin was closely appressed to the bone in this area, as several earlier workers (Lull 1903; Brown 1914a; Lambe 1904b) assumed.

In Eoceratops, as in all other ceratopsids, it seems highly unlikely that the dorsal surface of the frill was covered by musculature. In UA 40, the dorsal surface of the median parietal bar is highly vascularized, in contrast to the floor of the supratemporal fossa, which is smooth and bordered by a distinct ridge. The prominence of this ridge is exaggerated by crushing, but since it coincides with a change in surface texture, it is assumed that the ridge is not entirely a post-mortem effect. (This area is not preserved on the right side of the skull.) Lateral crushing has distorted the frill of UA 40 considerably and the posterior part of the frill, containing the fenestrae, is missing. Therefore, estimation of the extent of the supratemporal fossae is difficult. Nonetheless, the preserved parts of these fossae and the associated adductor passages are very large, indicating large and powerful adductor muscles. The inner walls of the adductor passage are smooth and somewhat flattened, indicating that the entire passage was filled with muscle fibres (see above). There is no indication of division into _medialis_ and _profundus_ portions at the area of origin but the assumed size of the muscle mass, as well as indications in the area of insertion (see below), suggest at least partial subdivision.

A large part of the area of origin for these two muscles consisted of the floor of the supratemporal fossa, formed by the parietal, but other areas bordering the supratemporal fossa were involved as well. Anteriorly, the median parietal bar projects laterally as a thin wedge, smooth below and heavily vascularized above, that overhangs the antero-lateral portion of the supratemporal fossa. Anterior and ventral to this projection there is a posterior projection of the postorbitals that braces the median parietal bar. The smooth ventral surfaces of both these projections probably participated in the origin of the _M_.

adductor mandibulae externus. In life, there may have been a broad temporal fascia connecting the thin lateral edge of the median parietal bar and the thin medial edge of the squamosal and covering the supratemporal fossa, which gave rise to some of the fibres of the *pars medialis* and *pars profundus*. The lateral (squamosal) wall of the fossa probably gave rise to the most lateral fibres of this muscle mass, as in *Sphenodon* (Haas 1973).

In modern sauropsids possessing a Bodenaponeurosis, the *M. adductor mandibulae externus medialis* inserts on the external surface of this tendon and the *pars profundus* inserts on the medial surface (Haas 1973). The Bodenaponeurosis itself inserts on the coronoid process, when such a process is present.

Haas restored the *pars superficialis* of *Protoceratops* inserting on the coronoid process (see above) but the *pars medialis* and *profundus* inserting "into the large inframandibular canal, as in the crocodiles" (Haas 1955, p.18). In ceratopsids, however, Haas felt that the major mass of the *M. adductor mandibulae externus* inserted on the coronoid process. (Haas postulated an expansion of the ?*pars profundus* at the expense of the ?*pars medialis* in ceratopsids, but since his arguments are based on an interpretation of the frill that is rejected here, and since, according to the present interpretation, there is no indication of a division in the area of origin of the muscle mass arising from the supratemporal fossa, the theory of an expanded *pars profundus* is rejected here as well.)

Ostrom (1964*a*, p.15) felt that "from a purely mechanical point of view, it would seem more probable that the bulk of the adductor externus fibers were applied against the dorsal extremity (rather than the base) of the prominent coronoid process" in *Protoceratops* and that "this most certainly was the point of attachment of the principal adductor in the higher ceratopsians with their much larger and higher coronoid processes". Nonetheless, Haas' reconstruction of the insertion of the *pars medialis* and *pars profundus* of *Protoceratops* is supported by osteologic features, as Ostrom himself acknowledged, and by comparisons with modern crocodilians (Haas 1955; Schumacher 1973). As well, the jaw mechanics of protoceratopsids are rather different from those of ceratopsids (see below), so Ostrom's application of similar mechanical requirements may not be justified. In ceratopsids, there is abundant evidence for the insertion of the *pars medialis* and *pars profundus* on the coronoid process, although the area of insertion must have been somewhat more extensive than that envisioned by Ostrom, who limited it to "the summit" of the coronoid process. As Frost (1973, p.360) has pointed out, tendons do not insert on small, sharply circumscribed regions of bone but "rather a large fan-out of collagen fibers distributes the tension load widely over the bone and even over adjacent fascia, so that the Sharpey's fiber mechanism functions far below its safety limit". Further, and this point is especially applicable to a strong tendon such as the Bodenaponeurosis, "the greater the total tension loads transferred thereby [*i.e.*, by Sharpey's fibres], the greater the fan-out" of collagen fibres (Frost 1973, p.361). Therefore, although it may be convenient to treat an insertional area as a single point in a biomechanical analysis, it is important to remember that in reality the insertion must cover an area proportional to the tendon's strength.

The adductor fossa in the lower jaw of ceratopsids is relatively much smaller than in *Protoceratops*, and the coronoid process is relatively much taller. Thus it seems likely that the bulk of the *M. adductor mandibulae externus* fibres inserted on the dorsal part of the coronoid process, rather than at its base and in the adductor fossa, as in *Protoceratops*. In both UA 40 and NMC 1254e, the medial surface of the dorsal part of the coronoid process is poorly preserved, with none of the external surface remaining. Also, the dorsal edge of the coronoid process is missing in UA 40 and although it is partially preserved in NMC 1254e, neither specimen shows the area of insertion of the *pars medialis* and *pars profundus* of the *M. adductor mandibulae externus*. In order to restore these muscles for *Eoceratops*, therefore, one must examine other ceratopsids.

In ROM 4519 (*Centrosaurus apertus*), the lower jaws are complete and extremely well preserved, showing scars on the dorsolateral surface of the coronoid process for the reception of the *pars superficialis*. The fibres of the *pars* *medialis* probably merged with those of the *pars superficialis* for there is no indication on the coronoid process of a tendinous division between the two portions. The coronoid bone is preserved intact and *in situ* in this specimen, with its lateral surface, which projects above and behind the coronoid process, showing deep striations that parallel those on the lateral surface of the coronoid process. These scars received fibres from the *pars profundus* but the bulk of the fibres of both the *pars medialis* and *pars superficialis* probably inserted on the dorsal edge of the coronoid process, and part of the dorsolateral surface of the coronoid bone, *via* the Bodenaponeurosis. Such an insertion would be strengthened further by the fact that the attachment of the Bodenaponeurosis lay above the suture between the coronoid and the coronoid process. Frazzetta (1968, p.148) has noted that "muscles tend to attach to bones in such a way that the major force component of contraction is directed roughly tangentially to the bone surface, and is hence balanced by tension in the surrounding periosteum". There are exceptions to this generalization, but these "are fewest in cases where there is is a *tendinous* attachment to a bone and where, therefore, a concentration of muscular force on a relatively small area would occur" (Frazzetta 1968, p.148). Muscular force can be resolved into components that are perpendicular and tangential to the surface of attachment. The perpendicular component "presumably is resisted only by [the] tensile strength of

Sharpey's fibers in the attachment site, by forces at the interface of each such Sharpey's fiber and surrounding bone, whereas the tangential component, in addition to these, is resisted by tensile strength in the surrounding periosteal sheet" (Frazzetta 1968, p.150). In the arrangement postulated for the Bodenaponeurosis of ceratopsids, a large fraction of the contractile force would be counteracted in the periosteum on the contacting surfaces of the coronoid and the coronoid process and thus the attachment of the tendon would be very strong. Some fibres of the *pars profundus* probably attached directly to the lateral surface of the coronoid rather than to the medial surface of the Bodenaponeurosis. The deep striations on this surface indicate a tendinous attachment and these fibres also would have a tangential relationship to the surface of the bone, and thus a very strong attachment. As further evidence to support such a restoration, it may be noted that the tendons of some powerful muscles, such as the *M. pterygomandibularis* of lizards, *do* attach to sutures rather than to a smooth bone surface (Frazzetta 1968).

The area of attachment of the Bodenaponeurosis in *Triceratops* shows a similar condition, although the coronoid is reduced and lies in a more posterior position than in *Centrosaurus* (Brown and Schlaikjer 1940*a*). In USNM 4276 (*Triceratops sulcatus*), the coronoid is completely fused onto the coronoid process but there is still a dorsal groove between the two elements (see Hatcher, Marsh and Lull 1907, pl. VI, fig. 1). Although the *pars profundus* of *Triceratops* must have inserted almost entirely on the Bodenaponeurosis, there are scars on the dorsomedial surface of the coronoid of USNM 4276, indicating that some fibres attached directly to this element.

The coronoid of *Eoceratops* is unknown, so the exact configuration of the insertion of the *pars profundus* is not certain, but the basic pattern of the insertion for the *pars medialis*-Bodenaponeurosis-*pars profundus* complex probably was similar in all ceratopsids, as *Centrosaurus* and *Triceratops* are not closely related (see below); hence a similar pattern is assumed for *Eoceratops*.

The large adductor passage and broad surface for the origin of the *pars medialis* and *pars profundus* of the *M. adductor mandibulae externus* indicate that these were the largest and most powerful muscles in the ceratopsid skull. Nonetheless, other muscle groups that were important functional components of ceratopsian skulls have left visible traces in fossil specimens.

In modern sauropsids, the *M. adductor mandibulae internus* is divided, in all cases, into an anterior *M. pseudotemporalis* and a posterior *M. pterygo-mandibularis*, although these muscles, especially the *M. pterygo-mandibularis*, may be divided further in a relatively complex fashion (Haas 1955). The *M. pterygo-mandibularis* generally is termed the "*M. pterygoideus*" but as Säve-Söderberg (1945, p.19) has pointed out: "the really correct application in

Reptiles of the term pterygoideus is uncertain, and its current use in lower Tetrapods [is] highly variable and confused." Therefore, Säve-Söderberg follows the practice of Luther, Lakjer and other anatomists in using "independent natural terminology" for this muscle, to avoid implications of homologies that are highly uncertain, re-introducing the term "*pterygo*-*mandibularis*", which had been used by earlier anatomists (Säve-Söderberg 1945).

Among modern sauropsids, such as *Sphenodon*, birds and many lepidosaurs, the *M*. *pseudotemporalis* is divided into a *M*. *pseudosuperior* and a *M*. *pseudoprofundus*, but in the akinetic Chelonia and Crocodilia this muscle is undivided (Haas 1955). Haas (1955) assumed that ceratopsians, which show no kinetic ability of the skull, also possessed an undivided *M*. *pseudotemporalis*, although the highly kinetic snakes have an undivided *M*. *pseudotemporalis*, so that the assumption is somewhat arbitrary. According to Haas (1955), there are no osteologic features indicating a divided *M*. *pseudotemporalis* in *Protoceratops* but since even major muscle divisions are not reflected invariably in skeletal features (Säve-Söderberg 1945), it is possible that this muscle was divided in ceratopsians. (Ostrom (1964*a*) restored a single *M*. *pseudotemporalis* for *Triceratops*, as well.)

In determining the area of origin of the *M*. *pseudotemporalis* it is necessary to identify the exit of the maxillary branch of the trigeminal nerve from the braincase. The *M*. *adductor* *mandibulae* *internus* is defined as lying anterior or medial to the maxillary branch (Säve-Söderberg 1945) and therefore, the exit of this nerve marks the most posterior limit of the adductor internus, "at least at the level of the emerging nerve" (Haas 1955, p.6).

In ceratopsians, as far as is known, the maxillary and mandibular branches share a common exit from the braincase but the ophthalmic branch has a separate foramen, as in crocodiles (Haas 1955; Romer 1956). The common exit for the maxillary and mandibular branches in *Protoceratops* is behind and slightly below the exit for the ophthalmic branch (see Brown and Schlaiker 1940*c*, fig. 15) but both foramina are close to the posterior border of the orbit, so that the *M. pseudotemporalis* must have arisen "towards the posterior orbital area, a rather surprising position in a reptile, where this muscle is generally found in the temporal region, covered laterally by the adductores externi" (Haas 1955, p.7). Such a position is not without precedent in the Sauropsida, however, since the *M. pseudotemporalis* of birds generally arises behind and below the orbit and Lakjer described an antorbital position for this muscle in the parrot *Aprosmictus cyanopygius* (Haas 1955). Haas (1955, p.7) placed the origin of the *M. pseudotemporalis* of *Protoceratops* "at the posterior part of the orbita ... The slightly developed decensus of the frontals and the anterior upper parts of the laterosphenoid form an arcade-like surface and thus an adequate origo surface for a rather moderately developed pseudotemporalis". This origin places the *M. pseudotemporalis* anterior to both foramina containing branches of the trigeminal nerve, but since the ophthalmic branch passes anteriorly, and presumably lay medial to this muscle, this restoration complies with Lakjer's definition of the *M. adductor mandibulae internus* (Säve-Söderbergh 1945).

For most ceratopsian genera, details of the braincase are not known. Hay (1909, pl. I, figs. 1 and 2) figured the external surface of the braincase of USNM 2416 (*Triceratops serratus*) and USNM 4286 (*T. sulcatus*). In both specimens, the common exit for the maxillary and mandibular branches lies behind and somewhat below the exit for the ophthalmic branch, both foramina lying a short distance posterior to the orbit. Again, in both specimens, as in *Protoceratops*, the laterosphenoid forms a sloping shelf that probably gave rise to the *M. pseudotemporalis*. Since the braincase of ceratopsians tends to be thoroughly coössified (Hay 1909), it is not possible to tell if there is a decensus of the frontals participating in the area of origin of the *M. pseudotemporalis* in these two specimens of *Triceratops*.

The element termed here the "laterosphenoid" is labelled "alisphenoid" by Hay (1909). In many descriptions of reptile skulls, there is some confusion as to the identification of this bone. According to Bellairs (1949), the laterosphenoids (or pleurosphenoids) of reptiles are ossifications of the pila antotica and are part of the true side wall of the cranial cavity. Thus, these bones should be distinguished from the alisphenoids of mammals, which most authors consider to be ossifications of the ascending process of the palato-quadrate (epipterygoid), secondarily incorporated into the braincase (Bellairs 1949). Not all workers agree with this identification (for example, Shaner 1926) but it is followed here in accordance with the views of Bellairs (1949) and Romer (1956).

In UA 40 (*Eoceratops*), both trigeminal foramina are far forward with a strong arch formed by the laterosphenoid passing from the anterior edge of the (presumed) exit of the maxillary and mandibular branches to the cranial roof, immediately posterior to the orbit. There is only a slight decensus of the frontals at this point so whereas the frontals may have participated in the origin of the *M. pseudotemporalis*, the main area of origin was provided by the laterosphenoid. As in *Protoceratops*, there is no indication of division of the *M. pseudotemporalis* in this area.

In *Sphenodon* and lizards, the divided *M. pseudotemporalis* inserts on the medial surface of the Bodenaponeurosis and on the more posterior extremities of the jaw (Haas 1973) but Haas (1955) reconstructed the insertion of the *M. pseudotemporalis* of *Protoceratops* farther forward, on the low, broad, anterior slope of the coronoid process, giving the muscle a more or less vertical orientation. (Given the anterior position of the origin of this muscle, in all ceratopsians, it is unlikely that the

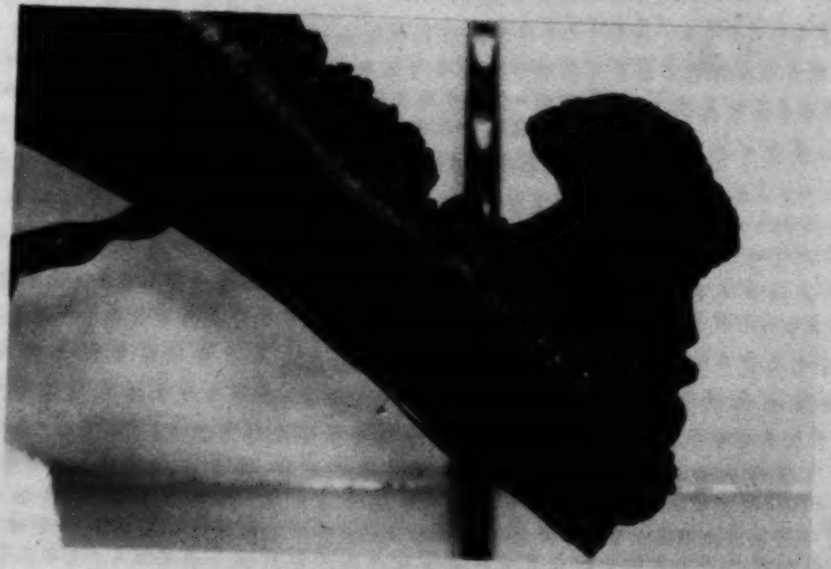
M. pseudotemporalis inserted on the posterior slope of the coronoid process, as the resulting orientation would produce a strong protraction of the jaw, a movement that would be blocked by the relationship of the rostral and predentary (see below).) Since Haas (1955) rejected the idea of a ceratopsian cheek, reconstructing instead a large infralabial gland in the depression lateral and ventral to the dentary teeth, he felt that the insertion of the *M. pseudotemporalis* could have spread along the dentary to act as a "gland compressor". According to the present interpretation, this area in all ceratopsians was occupied largely by fibres of the *M. levator anguli oris* and so the *M. pseudotemporalis* could not act as a gland compressor. Nevertheless, it is possible that the fibres of this muscle fanned out medial to the cheek muscle, having a large, long surface of attachment on the dentary.

Ostrom (1964*a*, p.16) reconstructed the insertion of the *M. pseudotemporalis* of *Triceratops* on the anterior slope of the coronoid process but added that "the insertion is still open to question and may actually have been more intimately associated with the summit of the coronoid process". In *Eoceratops*, in both UA 40 and NMC 1254e, the anteromedial face of the coronoid process forms a smooth, broad curve that intersects the anterior edge of the coronoid process and the dentary ridge at an acute angle. This surface probably represents the major area of insertion of the *M. pseudotemporalis*, although in neither specimen is the surface preserved well enough to show muscle scars. Ceratopsids also possess an anterior hook-shaped process on the coronoid process that is a feature more or less unique to this family. Among members of the Ceratopsidae, there are minor differences in the development of this process but basically, it is rather uniform in all ceratopsids. In UA 40, part of this process is preserved and most of it is preserved in NMC 1254e. NMC 1254e shows that the curved lateral surface of the process is marked by distinct striations that are deepest dorsally. This heavily striated surface is separated from the rest of the lateral surface of the coronoid process by a distinct ridge that again, is highest dorsally. The antero-lateral surface of the hook-shaped process forms an obtuse angle with the rest of the lateral surface of the coronoid process. This surface could represent the insertion of a separate, anterior slip of the *M. adductor mandibulae externus superficialis*, or even of the *pars medialis*. The striations are parallel to those marking the rest of the lateral surface of the coronoid process and the postulated areas of origin of the *pars medialis* and *pars superficialis* are directly adjacent to the hook-shaped process. On the other hand, the surface could represent the insertion of a separate, superficial portion of the *M. pseudotemporalis*. Since neither the *M. pseudotemporalis* nor the superficial and medial portions of the *M. adductor mandibulae externus* show indications of a division of muscle fibres at their origin, it is difficult to decide which muscle produced a separate slip to insert here. The surface of this process is small but the process itself is quite thick and the striations are prominent, indicating a tendinous insertion that concentrated a considerable contractile force on this small area. The *pars superficialis* and *pars medialis* of the *M. adductor mandibulae externus* of ceratopsids were certainly much larger muscles than the *M. pseudotemporalis*, so while it is possible that this process developed to increase the surface of attachment, and hence the power of the *M. pseudotemporalis*, it seems more likely that it served as a point of attachment for part of the *M. adductor mandibulae externus* (Fig. 14a).

The *M. pterygo-mandibularis* of modern sauropsids often is highly complex (Haas 1955). Both crocodilians and birds have separate *dorsalis* and *ventralis* portions of this muscle, and these portions may be subdivided further (Haas 1955). According to Haas (1955, p.8): "the striking similarity of the muscular arrangement in birds and crocodiles shows the close relationship of both groups, in spite of the difference in the state of kineticism, of generally different proportions of both types of skulls, and of the divergent development of the bony roof of the mouth. This correspondence in the muscular arrangement is certainly due to divergent development from a common, generalized, archosaurian ancestor." While it is possible that this similarity is due to convergence, and thus throws no light

Fig. 14. a. Lateral view of anterior, hook-shaped process on coronoid process of right dentary of ROM 4519 (*Centrosaurus apertus*). b. Medial view of right dentary of UA 41 (*Centrosaurus* sp.) showing scars on the dorsal and posterior surfaces of the coronoid process, marking the site of attachment of the Bodenaponeurosis.

a.



b.

on the condition in ceratopsians, Haas (1955) has provided convincing evidence that *Protoceratops* also shows a basic *dorsalis*-*ventralis* split in the *M*. *pterygo*-*mandibularis*.

Haas (1955, p.9) derived a long head of the *M*. *pterygo*-*mandibularis* ("*pterygoideus*" in Haas' terminology) from "a deep excavation rostromedially of the pterygoid prominence" and from the medial edge of that prominence. A shorter head would have arisen "from a deep excavation of the ventral surface of the pterygoid bone, where it sends a long flange towards the quadrate". According to Haas (1955), the long head would have inserted on the flattened lateral surface of the angular, while the short head inserted on a ridge ventral to the inframandibular channel. These two heads would have formed the *M*. *pterygo*-*mandibularis* *ventralis* while a third, *dorsalis* head arose from a smooth, trough-like depression on the dorsal surface of the pterygoid-ectopterygoid prominence and inserted on the medial surface of the short retro-articular process (Haas 1955). Although in some modern sauropsids, the *pars* *dorsalis* is subdivided, Haas (1955, p.9) felt that "the whole configuration of the palate and the increased distance between the articular facet of the quadrate and the basis cranii preclude the existence of a second pterygoideus dorsalis muscle, which should arise from the basis cranii."

Ostrom (1964*a*, p.18) treated the *M*. *pterygo*-*mandibularis* as a single functional unit arising from "the posterior surface of the ventral wing of the pterygoid and along the ventral margin of that process" and inserting "on the ventro-lateral, ventral and ventro-medial surfaces of the rear of the mandible adjacent to the articulation." Ostrom's reconstruction is not as detailed as that of Haas but does not differ from it substantially.

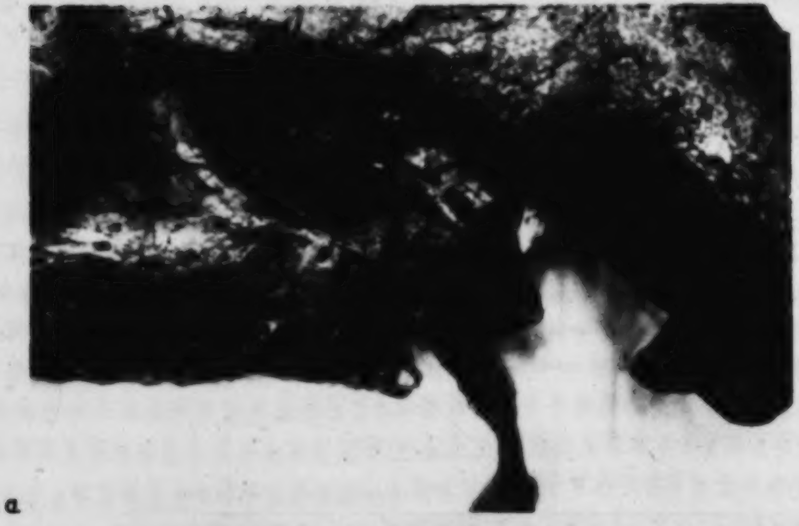
In *Eoceratops*, the possible areas of origin of the *M. pterygo-mandibularis* are preserved only in UA 40. In comparison with *Protoceratops*, the available areas of origin are much reduced in *Eoceratops*. *Eoceratops* lacks the depression anterior to the pterygoid-ectopterygoid process seen in *Protoceratops* and instead there is a thin ridge running from the basicranial articulation to the quadrate that seems to have formed the origin for both the long and the short heads of the *M. pterygo-mandibularis ventralis*. This ridge is formed entirely by the pterygoid and the quadrate process of the pterygoid. There is no indication of separate long and short heads, although there is a depression above the medial half of the ridge that might have housed the long head and possibly, there was only a single *pars ventralis* in *Eoceratops*. The medial portion of the ridge is dorsal to the area giving rise to the long head in *Protoceratops* so that either this head has shifted its origin in *Eoceratops*, to merge with the short head, or it has been lost altogether.

The ectopterygoid of all ceratopsids, including *Eoceratops*, is a small element that is more or less completely fused onto the pterygoid. This bone forms a rugose knob that provided the area of origin for the *M. pterygo-mandibularis dorsalis*. Immediately behind this knob there is a smooth, trough-like depression over which the *pars dorsalis* passed to curve around the posterior edge of the pterygoid-ectopterygoid process and insert on the medial surface of the retro-articular process (Fig. 15a, b). Although the ectopterygoid of ceratopsids is relatively smaller than that of protoceratopsids, the area of origin of the *M. pterygo-mandibularis dorsalis* is relatively much larger, indicating a more powerful muscle. The rugose nature of the ectopterygoid indicates at least a partially tendinous attachment and again, the attachment of the fibres to the surface of the bone would be more or less tangential: a strong attachment, indicating a relatively powerful muscle. (Given the relative positions of the two heads of the *M. pterygo-mandibularis* in *Eoceratops* and *Protoceratops*, it would be more appropriate to reverse the designations "*dorsalis*" and "*ventralis*", but I am inclined to retain this terminology, if only for the sake of easy comparison with Haas' restoration.)

None of the presumed areas of insertion of the *M. pterygo-mandibularis* is preserved in either UA 40 or NMC 1254e so, again, it is necessary to use other ceratopsids in order to reconstruct these insertions in *Eoceratops*.

The angular of ROM 4519 (*Centrosaurus apertus*) has a smooth, concave lateral surface bounded ventrally by a ridge marked by short, but very distinct muscle scars (Fig. 16).

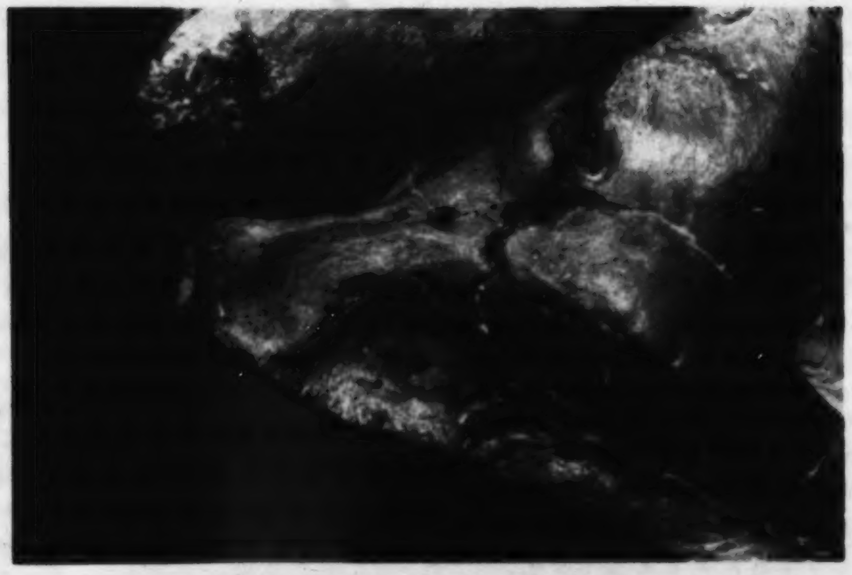
Fig. 15. Lateral view of left ectopterygoid, showing area of origin of the *pars dorsalis* of the *M. pterygomandibularis*, in a. AMNH 6325 (*Pentaceratops sternberghii*) and b. AMNH 5239 (*Centrosaurus flexus*).

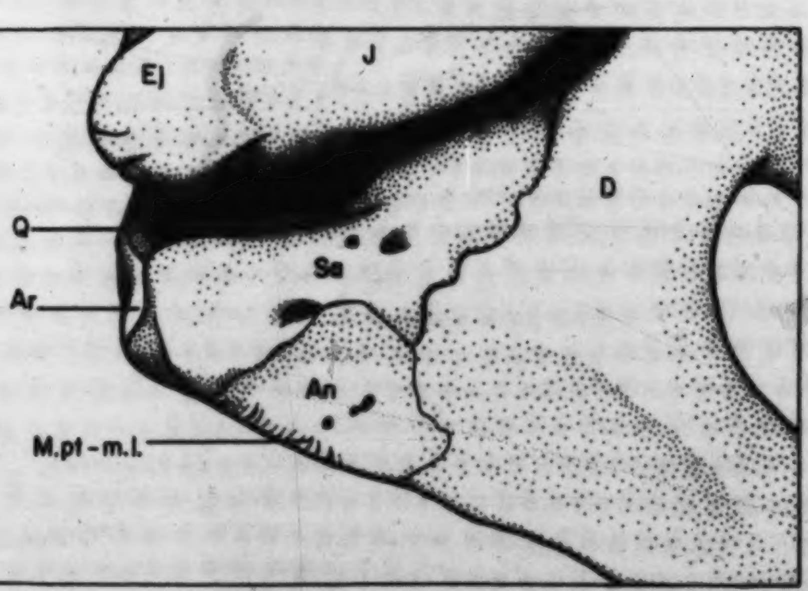


a

b

Fig. 16. Lateral view of right ramus of lower jaw of ROM 4519 (*Centrosaurus apertus*) showing the scars from the insertion of the long head of the *M. pterygomandibularis* on the angular.




Ej
J
D
Q
Sa
Ar
An
M.pt-m.l.

This area, relatively much larger than in *Protoceratops*, received the fibres of the long head. The smooth surface of the angular indicates a fleshy insertion but the distinct ventral scars indicate that at least some of this attachment was tendinous. As in *Protoceratops*, there is a ridge beneath the inframandibular fossa that would have received the fibres of the short head, although this area is relatively restricted with respect to that of *Protoceratops* (see Brown and Schlaikjer 1940*a*, fig. 1B for an illustration of this area in AMNH 5351 (*Centrosaurus nasicornus*).) As in *Eoceratops*, the areas of origin, which are extremely similar to those of *Eoceratops*, show no indication of separate long and short heads but there are two distinct areas of insertion for the *pars ventralis* so that this muscle probably was divided, at least distally. Compared with *Protoceratops*, the long head assumed greater importance, judging from the area of insertion.

The retro-articular process of ceratopsids is relatively longer than that of *Protoceratops* and may have provided a slightly larger area of insertion for the *pars dorsalis*.

Various workers, beginning with Dollo (1884), have associated an anterior portion of the *M. pterygomandibularis* with the antorbital fenestra of archosaurs. Some authors, such as Anderson (1936), have maintained that the fenestra provided room for this muscle to bulge upon contraction, while others (for example, Gregory 1951) felt that the margins of the fenestra provided an area of muscle attachment. Whatever the function of the antorbital fenestra, and Reig (1970) has suggested that none of the proposed explanations are adequate, it could not have been associated with the *M*. *pterygo*-*mandibularis* in ceratopsians. Dollo (1884) noted that small "*temporalis*" (*i*.*e*., *adductor mandibulae externus*) muscles, a large "*pterygoideus*" and a large antorbital fenestra appear to have been correlated in archosaurs, so he assumed that a correlation existed between the *M*. *pterygo*-*mandibularis* and the antorbital fenestra. In modern crocodilians, however, the antorbital fenestra is lost but the *M*. *pterygo*-*mandibularis* is strong, attaching to the inner surface of the preorbital region of the skull (Gregory 1951). Ewer (1965, p.419) therefore assumed that the primary function of the antorbital fenestra could not have been as an area of attachment, although it could have functioned to permit lateral bulging, this function perhaps being "taken over by the large palatal fenestrations which are present in Crocodilia", although the structure of the antorbital fenestra does not suggest either function (Ewer 1965). The function of the anterior division of the *M*. *pterygo*-*mandibularis* in crocodilians is to provide "the powerful bite with the jaws widely open which is neccessary for coping with large prey", (Ewer 1965, p.419). Such a function would not be neccessary in ceratopsians, which did not need to grasp struggling prey, so it is reasonable to assume that an anterior slip of the *M*. *pterygo*-*mandibularis* was not present. Also, contraction of such a muscle produces a powerful anterior and dorsal motion in the jaws (Walker 1961) and, as mentioned above, the form and relationship of the rostral and predentary preclude such motions in ceratopsids.

In all crocodilians (Schumacher 1973), in the ostrich (Säve-Söderberg 1945) and, rarely, in chelonians (Schumacher 1973), there is a third division of the *M. adductor mandibulae internus*, the *M. intramandibularis*. The presence of this muscle in both crocodilians and in the ostrich has led to the suggestion that a similar condition existed in at least the primitive archosaurs, if not in all archosaurian genera (Säve-Söderberg 1945). (Neither Haas (1955) nor Ostrom (1964*a*) discussed this muscle.) Where present, the *M. intramandibularis* gathers the fibres of the *Mm. pseudotemporalis* and *pterygo-mandibularis*, *via* a tendon, and inserts *via* another tendon into the adductor fossa of the lower jaw (Schumacher 1973). In crocodilians, the *M. intramandibularis* acts to stretch the other muscles of the *adductor mandibulae internus* group, allowing a quick, strong contraction (Schumacher 1973). In ceratopsians, however, rapid contraction of the jaws would not be as important as the pressure exerted upon occlusion (see below) so that a mechanism to stretch the fibres of the *M. adductor mandibulae internus* to their utmost would be unneccessary.

According to Säve-Söderberg (1945, p.33):

"not improbably, a strong development of the M.

> intramandibularis is at least one of the factors causing the fenestration in the lateral wall of the mandible in the _Crocodilia_ [_sic_]. Next to the fenestra is the distal end of the comparatively long add. externus profundus ... which may not need so much space for swelling within the mandible, but medially to that (and to the r. mandibularis V) there is the very short most posterior portion of the m. intramandibularis ... The contraction of this muscle portion must conceivably cause a lateral bulging of the add. externus profundus and thus indirectly of the membrane".

Although the lateral mandibular fenestra is typical of other archosaurs (Säve-Söderberg 1945), it is not characteristic of ornithischians in general (Romer 1956) and it is not found in any ceratopsian, probably because these forms lack a _M. intramandibularis_ and, at least in ceratopsids, none of the _M. adductor mandibulae externus_ inserts in the adductor fossa (see above).

The fact that ceratopsians had a fundamentally different type of feeding mechanism than do crocodilians, plus the lack of a lateral mandibular fenestra that would allow bulging of a _M. intramandibularis_ indicates very strongly that such a muscle was not present in ceratopsians.

The _M. adductor mandibulae posterior_ of sauropsids shows considerable variation. Haas (1955, p.11) assumed that there is a connection "between the degree of kineticism [of the skull] and the fission of the muscle into several portions. Nevertheless, the akinetic crocodiles have a bipartite add. posterior." With respect to _Protoceratops_, Haas felt that the muscle could be either single or divided, since the skull gives no indication of the complexity of this muscle. Haas (1955, p.11) gave the anterior slope of the quadrate and the arch above the quadrate as the origin of the *M. adductor mandibulae posterior* of *Protoceratops* and "the medial surface and lower margin of the splenial" as the insertion. Such an insertion would slightly overlap the Meckelian fossa and would be covered medially by the "short head" of the *M. pterygo-mandibularis ventralis* (Haas 1955).

Ostrom (1964*a*, p.17) specified a similar origin for the *M. adductor mandibulae posterior* of *Triceratops* but felt that this muscle "probably accounted for the bulk of the muscular fibres that must have inserted in and around the Meckelian fossa, as in crocodilians and certain lacertilians, with the major part of the external adductors inserting more superficially on the upper extremities of the coronoid process."

The presumed area of origin of the *M. adductor mandibulae posterior* in *Eoceratops* is preserved only in UA 40. The anterior face of the quadrate is broad and there is a slightly hollowed area on the ventro-lateral surface of the quadrate process of the pterygoid that probably also was involved in the area of origin. The Meckelian fossa is not preserved in UA 40, and it is only partially preserved in NMC 1254e, but the postero-lateral walls of this fossa in NMC 1254e show parallel striations that represent the insertion of the *M. adductor mandibulae posterior*. In ceratopsids, the *M. adductor mandibulae posterior* was the only muscle that inserted in the Meckelian fossa; hence, probably, the relative reduction of this fossa compared to that of *Protoceratops*, where the *pars medialis* and *pars profundus* of the *M. adductor mandibulae externus* inserted here (see above).

The constrictor internus dorsalis group of trigeminal muscles joins the braincase with the palatoquadrate region and with the lower eyelid (Haas 1955). Generally, in sauropsids, this group consists of a *M. protractor pterygoidii*, a *M. levator pterygoidii* and a *M. levator bulbi* (Schumacher 1973). The *Mm. levator* and *protractor pterygoidii* make possible intracranial movements in sauropsids with kinetic skulls. These muscles are well developed in birds, most lizards and snakes (Haas 1973), but are present only in the embryo in chelonians and are absent in crocodilians (Schumacher 1973). The condition in *Sphenodon* appears to be highly variable. In the opinion of Haas (1973) and of Ostrom (1962), this variability is ontogenetic, juveniles having somewhat kinetic skulls, while kinesis is lost in adults, in which the *Mm. protractor* and *levator pterygoidii* are poorly developed or absent (Haas 1973). Thus, among modern sauropsids, there is a strong correlation between the possession of these muscles and cranial kinesis.

Again, using the apparent fact that ceratopsian skulls are akinetic, Haas (1955) assumed that neither a *M. protractor pterygoidii* nor a *M. levator pterygoidii* was present in *Protoceratops*. All sauropsids except chelonians, however, have a well developed *M. levator bulbi* (Haas 1955), although the divisions of this muscle may vary.

In the earlier literature, there was considerable debate over the origin and relationships of the *M. levator bulbi* although now it is generally accepted as a derivative of the constrictor internus dorsalis group (Säve-Söderberg 1945). In modern sauropsids, the upper eyelid usually is more or less immobile, while the lower lid is larger and more mobile (Porter 1972; Welty 1962). The *M. levator bulbi* partly or entirely functions in depressing the lower eyelid and typically, the sauropsid *M. levator bulbi* consists of a *pars dorsalis*, attached to the lower lid, and a *pars ventralis*, inserting onto a palatal membrane ("Gaumenmembran") or onto the dermal bones of the palate (Säve-Söderberg 1945). Since both crocodilians and birds lack a *pars ventralis*, Haas (1955) restored a similar condition for *Protoceratops*. Haas (1955, p.4) gave two possible areas of origin for the *M. levator bulbi* of *Protoceratops*: "a bony ledge above the posterior foramen trigemini on the prootic could reasonably be interpreted as the origo crest for this muscle, but a more anterodorsally situated excavation at the anterior corner of the latero-sphenoid, at the same time the only possible origo area for the pseudotemporalis ..., is also a possibility." The insertion, in either case, would be along the entire rim of the lower lid, the muscle passing ventral to the *bulbus occuli* and then swinging dorsally to its area of origin

(Haas 1955). (Ostrom (1964*a*) restored only the muscles directly involved with mastication and so did not discuss the constrictor internus dorsalis group.)

Following Haas (1955), I assume that the *Mm. levator* and *protractor pterygoidii*, if present, were of minor importance in *Eoceratops*, as in all ceratopsians. With respect to the *M. levator bulbi*, the insertion, involving soft tissue, can only be assumed to be similar to that seen in modern sauropsids. The possible area of origin of the *M. levator bulbi* in *Eoceratops* is present only in UA 40. As in *Protoceratops*, there is a ridge on the laterosphenoid and on the prootic, but these ridges are more or less continuous, forming a smooth ledge. Considering the neccessarily convoluted line of action of the *M. levator bulbi*, it seems most likely that this muscle arose, in both *Eoceratops* and *Protoceratops*, from the anterior, laterosphenoid ridge. A more posterior origin would give a large retraction component to the contractile force of this muscle, and this component would be essentially useless as far as depression of the lower lid was concerned. In UA 40, there is a shallow depression anterior to the laterosphenoid ridge that probably also was involved in the area of origin. The origin of the *M. pseudotemporalis* would have been immediately posterior to the origin of the *M. levator bulbi*.

The final group of sauropsid muscles innervated by the trigeminal nerve, the constrictor ventralis trigemini group, consists of a single *M. intermandibularis* (*mylohyoideus*), which merges posteriorly with similarly oriented fibres innervated by the facial nerve. Together, these two muscles connect the two lower jaw rami. The *M. intermandibularis* can be single or divided in modern sauropsids. (Neither Haas (1955) nor Ostrom (1964*a*) restored this muscle.) The ventral edge of the dentary of UA 40 is not preserved but in NMC 1254e, the posterior part of the ventral edge of the dentary shows distinct muscle scars that probably were associated with the *M. intermandibularis*, although this muscle left no scars more anteriorly.

Finally, since its action is antagonistic to the action of the trigeminally-innervated jaw adductors, it is appropriate to discuss the facially-innervated *M. depressor mandibulae* in this section. Since the action of opening the mouth is accomplished largely by gravity, the *M. depressor mandibulae* is much smaller than the jaw adductors. In modern sauropsids, this muscle arises in the vicinity of the squamosal and inserts on the retro-articular process of the lower jaw (Haas 1955, 1973).

Haas (1955) reconstructed the origin of the *M. depressor mandibulae* of *Protoceratops* on the squamosal, in a smooth concave area extending dorsally to the level of the dorsal border of the lower temporal fenestra. The insertional area, on the retro-articular process is "somewhat U-shaped" in *Protoceratops*, producing a muscle "with two anteriorly sharpened edges or two completely distinct portions" (Haas 1955, p.22). According to Haas

(1955), such an arrangement would leave room for a tympanum, although Haas felt that the tympanum, and perhaps the whole middle ear, might have been missing in dinosaurs. Since the publication of Haas' reconstruction, Colbert and Ostrom (1958) and Ostrom (1961) have shown that stapes are present in certain dinosaurian genera and a tympanum probably was present in all dinosaurs.

Ostrom (1964*a*) restored the *M. depressor mandibulae* of *Triceratops* arising from the antero-ventral edge of the squamosal and inserting on the retro-articular process, so that the fibres are not nearly as vertical as in *Protoceratops*. Among ceratopsians, such a horizontal arrangement is possible only in ceratopsids, and varies with different genera even within the Ceratopsidae, where the squamosal is produced into a broad ventro-lateral flange that is not present in psittacosaurids or protoceratopsids. There is more room for a tympanum in ceratopsids than in protoceratopsids.

In *Eoceratops*, the area of origin of the *M. depressor mandibulae* is preserved in both UA 40 and NMC 1254a. In UA 40, the entire jugal notch is preserved. This notch is very narrow compared to that of many other ceratopsids and the *M. depressor mandibulae* must have been correspondingly shorter. There is a slight bulge in the center of the anterior edge of the squamosal, which is even more rugose than the rest of this edge and the medial surface of the squamosal immediately posterior to the bulge is considerably thickened and rugose, at least anteriorly. These surfaces formed the area of origin for the M. depressor mandibulae. In NMC 1254a, the anterior edge of the squamosal is slightly convex and roughened but is not developed as a conspicuous bulge as in UA 40. The bone in this area is thicker than in UA 40, however, so it seems that there was some variation in this area in Eoceratops.

The retro-articular process is not preserved in either UA 40 or NMC 1254 but the lower jaws of ceratopsids are fairly uniform so that one may estimate the relative position of this process in Eoceratops. As restored, the M. depressor mandibulae would have an orientation of about 45° with respect to the long axis of the maxillary tooth row.

Partial restorations of the cranial musculature of Eoceratops are given in Figs. 17, 18 and 19.

The cranial muscles of other ceratopsids appear to have been rather similar to those of Eoceratops, although the number of specimens of each species is so restricted that it is not possible to identify individual, ontogenetic or sexual differences and in many instances the proposed areas of attachment are lost, poorly preserved or unprepared. (This problem is especially acute with respect to the braincase, which seldom is prepared, and the lower jaws, which often are incomplete or missing altogether.) Nonetheless, it is possible to identify certain trends and variations.

In all ceratopsids there is a large passage for the

Fig. 17. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored, showing postulated appearance and placement of the *Mm*. *levator bulbi*, *levator anguli oris* and *depressor mandibulae*, x.20. (Note fascia covering lateral temporal fenestra.)

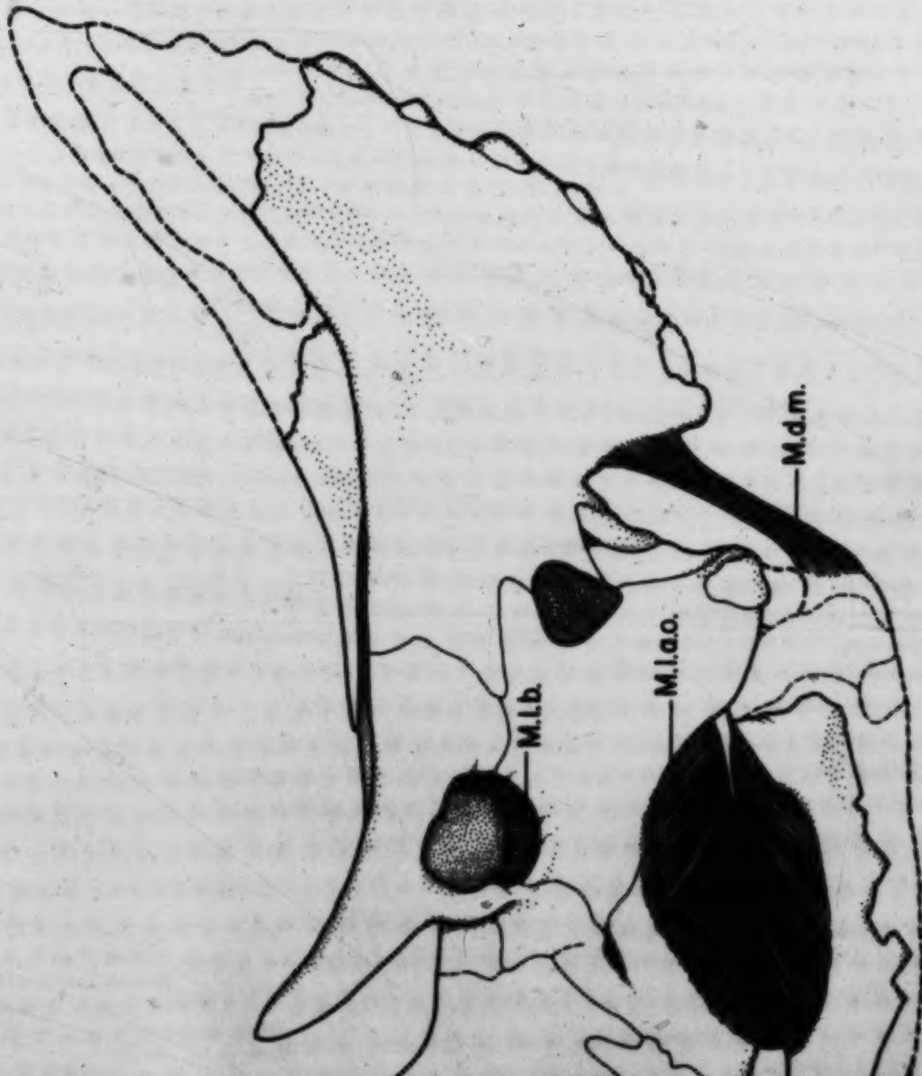

M.d.m.
M.l.a.o.
M.l.b.

Fig. 18. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored but with upper and lower temporal arches cut away and the *Mm.* *levator bulbi* and *levator anguli oris* removed to show postulated appearance and placement of *Mm.* *adductor mandibulae externus superficialis*, *adductor mandibulae externus medialis*, *pseudotemporalis* and *intermandibularis* and the long head of the *M.* *pterygo-mandibularis* and a possible separate anterior slip of the *M.* *adductor mandibulae externus superficialis*, x.20. (The muscle visible medial to the posterior orbital rim is the *M.* *pseudotemporalis*.)

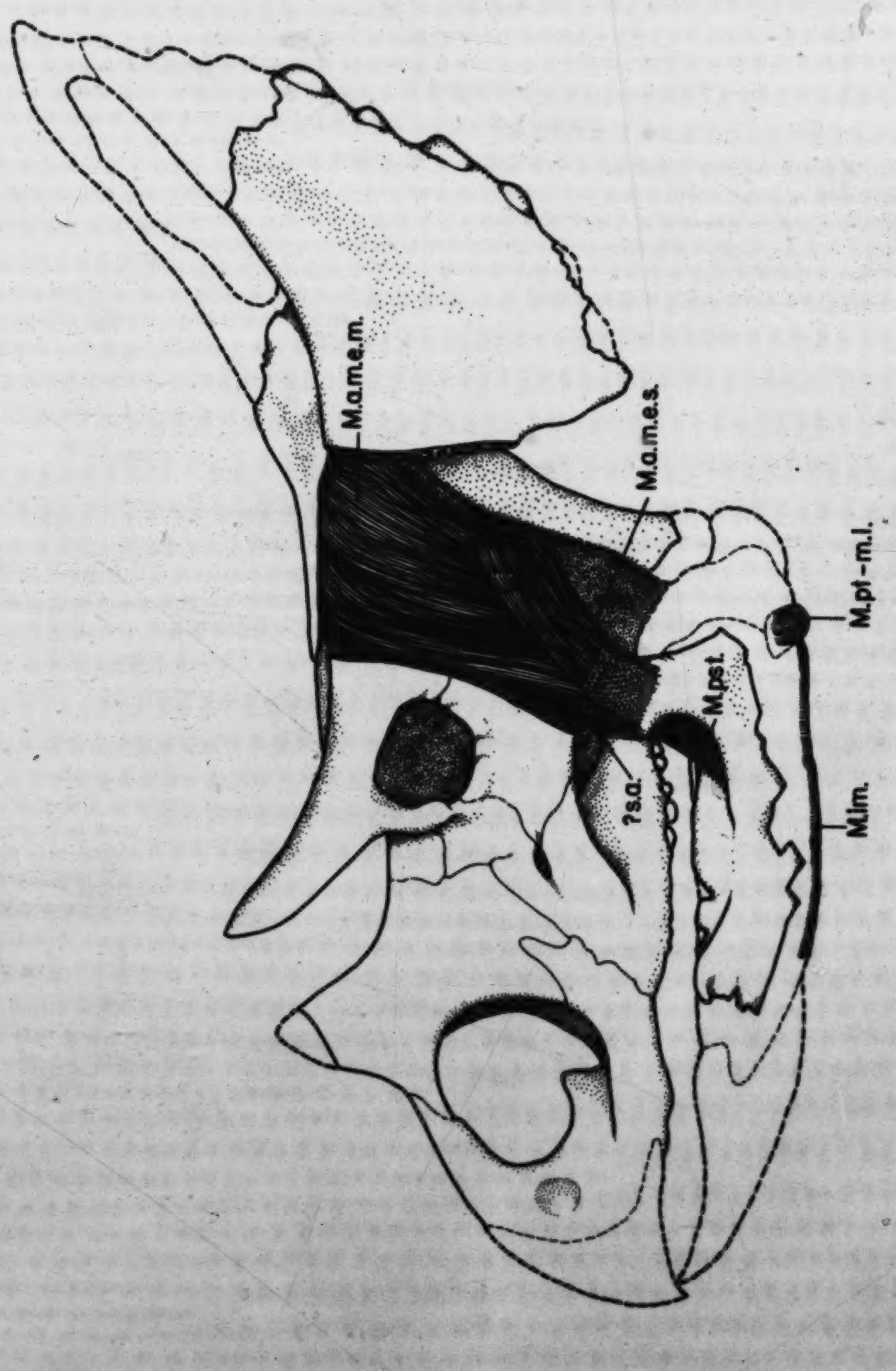
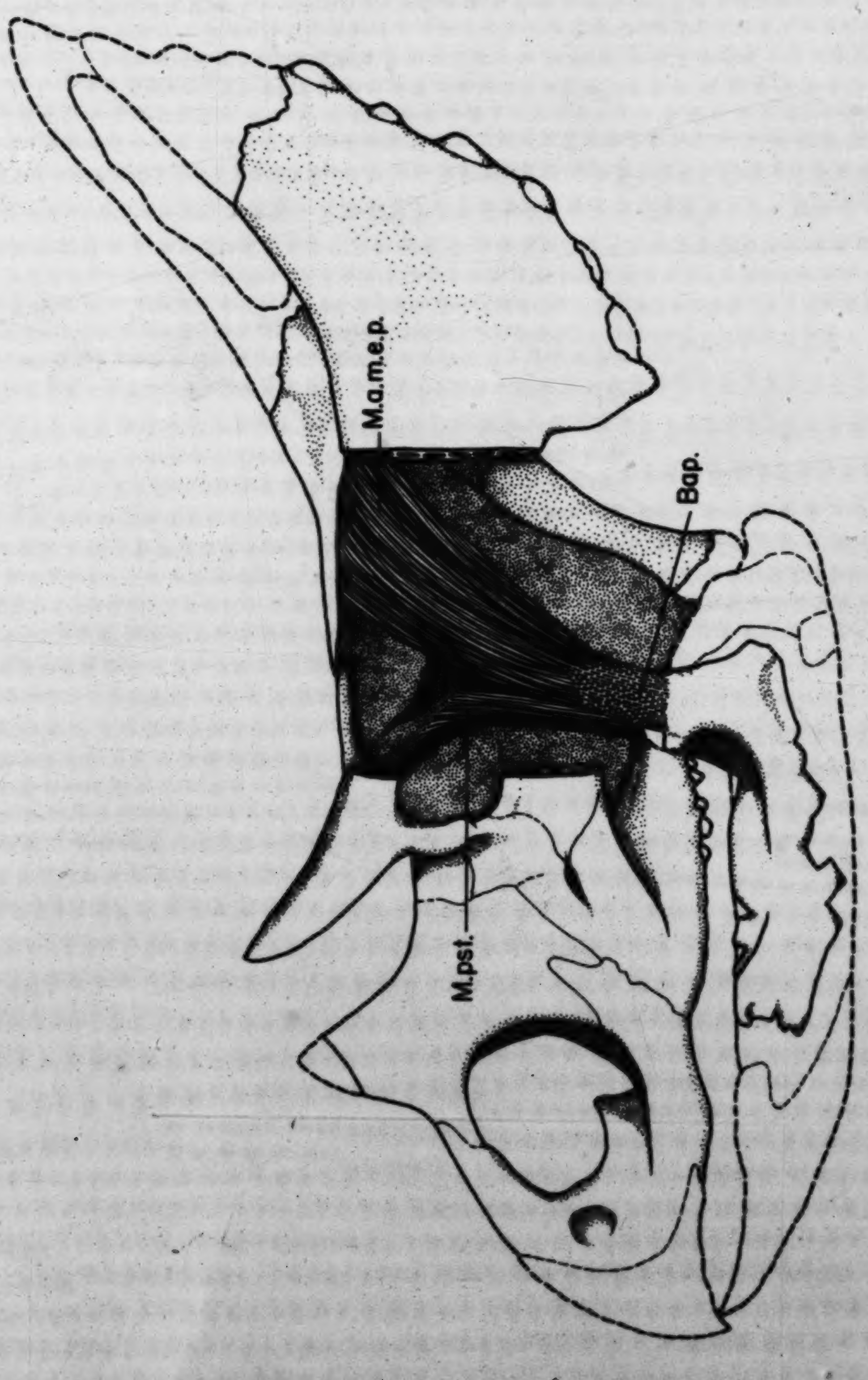

M.a.m.e.m.
M.a.m.e.s.
M.pt-m.l.
M.pst.
?s.a.
M.lm.

Fig. 19. Left lateral view of skull of UA 40 (*Eoceratops canadensis*), partially restored but with upper and lower temporal arches and much of orbital rim cut away and the *Mm. adductor mandibulae externus superficialis* and *adductor mandibulae externus medialis* removed to show postulated apperance and placement of the *Mm. pseudotemporalis* and *adductor mandibulae externus posterior* and the Bodenaponeurosis, x.20.


M.a.m.e.p.
Bap.
M.pst.

fibres of the *M. adductor mandibulae externus*, which, from its inferred size, formed the main jaw adductor in all ceratopsids.

In all ceratopsids, the lateral temporal fenestra is much reduced with respect to that of *Protoceratops* but there is considerable variation in its placement on the side of the skull. If this fenestra does mark the major area of origin of the *pars superficialis*, there must have been considerable variation in the length and direction of pull in this muscle, as well. *Eoceratops* is unusual in that the dorsal border of the lateral temporal fenestra is on a level with the ventral edge of the orbit. In most ceratopsids, this fenestra lies in a more ventral position on the side of the skull than in *Eoceratops* and sometimes, as in *Arrhinoceratops*, *Centrosaurus*, *Styracosaurus* and some species of *Triceratops*, it lies in a much more ventral position. In all these forms, the *pars superficialis* must have been shorter than in *Eoceratops*. In many species, for example, *Chasmosaurus brevirostris*, *C. belli* and most species of *Triceratops*, the area between the orbit and the lateral temporal fenestra is not so wide as in *Eoceratops* and the direction of pull of the *pars superficialis* would have been more vertical.

The area of insertion of the *pars superficialis* is visible in several ceratopsid specimens. This area always is relatively large and confined to the dorso-lateral surface of the coronoid process. It is possible, since the fibres of the *pars superficialis* and *pars medialis* seem to have merged into each other, that the *pars superficialis* was considerably reduced and that this area of insertion was occupied largely by the *pars medialis*. Since the *pars medialis* already had a large area of insertion on the lateral surface of the Bodenaponeurosis, however, and since it would seem to be advantageous to have all portions of the main jaw adductor as large and powerful as possible, it seems unlikely that the *pars superficialis* was greatly reduced. Due to the lack of osteologic evidence, however, it is not possible to be certain on this point. In no ceratopsid specimen is there any indication of a separate lateral portion of the *pars superficialis*, such as Haas (1955) reconstructed for *Protoceratops* and *Psittacosaurus*.

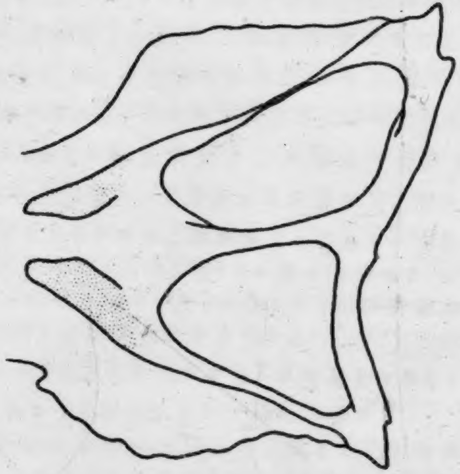
In some genera, especially *Anchiceratops*, *Arrhinoceratops* and *Pentaceratops*, the jugal-epijugal projection protrudes much further laterally than in *Eoceratops* but in none of these genera does this area appear to have served as an origin for a lateral portion of the *pars superficialis*. The ventral surface of these bones is not excavated as for a muscle attachment, and indeed, the epijugal shows deep vascular marks and may have had a horny covering in life. Further, a muscle arising from this area would have a strong postero-lateral component of contraction, an unlikely action for a jaw adductor.

All ceratopsids show strong maxillary and dentary ridges, here interpreted as the areas of insertion of the cheek muscle, the *M. levator anguli oris*. Presumably, this muscle arose from the medial surface of the jugal in all ceratopsids, but UA 11735 (*Centrosaurus* sp.) is the only skull on which I have observed suitable scars on the jugal.

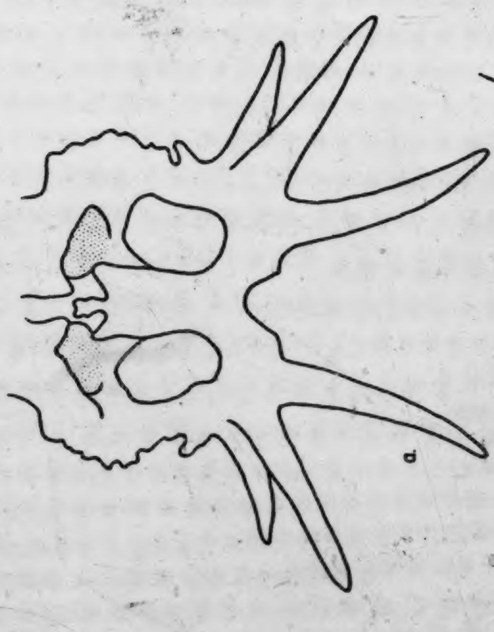
In no ceratopsid is there any indication that the *pars medialis* or the *pars profundus* of the *M. adductor mandibulae externus* extended farther than the posterior rim of the supratemporal fossa, but even after discounting post-mortem crushing, there is a certain amount of variation in the size and shape of the supratemporal fossae of ceratopsids and hence, presumably, in the muscles arising from it.

The supratemporal fossae of *Styracosaurus* are broad laterally but short antero-posteriorly (Fig. 20a). Although there is some variation in this feature, this fundamental shape also characterizes *Centrosaurus*. In these genera, the basic outline of the frill is broad and round, with the short squamosal sloping postero-ventrally toward the center of the lateral edge of the frill. The supratemporal fossa follows the medial edge of the squamosal for part of its length so that the area available for the origin of the *pars medialis* and *pars profundus* is broad but short, narrowing rapidly posteriorly. In *Chasmosaurus* (Fig. 20b), *Pentaceratops* and possibly *Eoceratops*, although lateral crushing has distorted the frill of UA 40, the supratemporal fossae are long and relatively narrow, especially in *Pentaceratops*, slanting postero-laterally along the medial edge of the long squamosal. *Arrhinoceratops* and

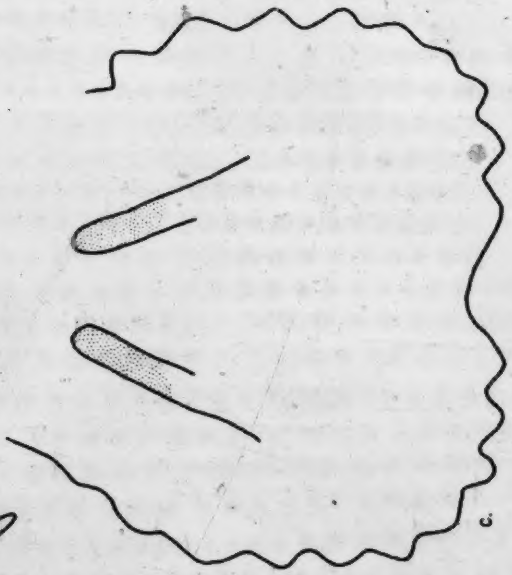
Fig. 20. Dorsal view of supratemporal fossae of a. NMC 344 (*Styracosaurus albertensis*), x.06 (from Lull 1933); b. AMNH 5402 (*Chasmosaurus belli*), a badly crushed skull but crushing is largely dorso-ventral and at least the left supratemporal fossa appears to be undamaged, x.07 (from Lull 1933); and c. YPM 1823 (*Triceratops serratus*), x.08 (from Hatcher, Marsh and Lull 1907).



b.



a.



c.

Anchiceratops have supratemporal fossae of approximately the same shape, but relatively shorter and more narrow.

Triceratops (Fig. 20c) shows some variation in this character, but approaches the long, rectangular shape more closely than the broad, triangular one. In some species, the supratemporal fossae may be short and narrow but the basic shape is rectangular.

Certainly such variations must have affected the origins of the pars medialis and pars profundus, although these muscles were large in all ceratopsids. Pentaceratops, for instance, has relatively much larger fossae than, say, Triceratops sulcatus and thus the area available for muscular attachment is relatively much larger, as well. The possible significance, if any, of these variations is obscure, and it is possible that the shape of the fossae responded to changes in the shape of the frill that were governed by demands other than those imposed by the adductor musculature.

As noted above, the exact placement of the insertion of the Bodenaponeurosis, pars medialis and pars superficialis may vary somewhat among ceratopsids, although the basic pattern seems to be similar in all genera, but too few genera possess complete, well preserved lower jaws to trace changes in this character throughout the group.

The M. pseudotemporalis appears to have been a very constant element in all ceratopsids. The braincase, as far as is known, is very similar throughout the Ceratopsia and the laterosphenoid always shows a strong oblique ridge that presumably gave rise to both the *M. pseudotemporalis* and the *M. levator bulbi*. The major area of insertion, on the anteromedial slope of the coronoid process, also is very constant among ceratopsids. Haas (1955, p.7) has restored the *M. pseudotemporalis* as "a flattened muscular ribbon" but there is ample room in all ceratopsids for a fairly thick muscle and the robust areas of origin and insertion tend to confirm this interpretation.

The pterygoid and ectopterygoid, and hence the *M. pterygo-mandibularis* of ceratopsids, are rather different than in *Protoceratops*. In all ceratopsids, the *pars dorsalis* arose from a rugose knob formed by the ectopterygoid, passed over a smooth, trough-like depression and inserted on the retro-articular process, which is relatively larger than in *Protoceratops*. All ceratopsids show two areas of insertion for the *pars ventralis*: one on the lateral surface of the angular and one on the short ridge bordering the Meckelian fossa. In most, however, there is no indication of division into two heads at the area of origin, as there is in *Protoceratops*, the ridge providing the origin for the *pars ventralis* continuing uninterrupted from the basipterygoid process to the quadrate.

The *M. adductor mandibulae posterior* also seems to have been a constant element in ceratopsids, arising from the broad anterior slope of the quadrate and inserting in the Meckelian fossa, the only ceratopsid muscle to occupy this fossa.

With the exception of the apparently variable size and shape of the *M. adductor mandibulae externus medialis* and *profundus* origins, and the possible variation in size and location of the *pars superficialis* origin, the *M. depressor mandibulae* probably was the most variable muscle in the ceratopsid skull. In all genera it arose from the anterior edge of the ventral squamosal flange, which usually shows a projection, thickening and/or rugosity to mark the area of origin. As mentioned above, the retro-articular process is preserved in only a few genera but it undoubtedly received the fibres of the *M. depressor mandibulae* in all ceratopsians. The main source of variation in this muscle involves its probable length and orientation in life. In *Eoceratops*, the *M. depressor mandibulae* appears to have been rather short, acting at more or less a 45° angle to the plane of the maxillary tooth row. *Chasmosaurus belli*, *C. russelli* and some species of *Triceratops* probably showed a similar condition but in *Chasmosaurus kaiseni* and *Pentaceratops*, the *M. depressor mandibulae* was much longer, acting at a somewhat steeper angle. In these latter forms, the quadrate is relatively longer and the ventral flange of the squamosal relatively shorter. *Centrosaurus*, *Styracosaurus* and some species of *Triceratops* probably were intermediate between these two extremes. *Chasmosaurus brevirostris* shows a rather different condition, suggesting a larger and more powerful *M. depressor mandibulae*. The anterior edge of the ventral squamosal flange of this species has a very large projection for the origin of the *M. depressor mandibulae* and this muscle appears to have been oriented at a steeper angle than in *Eoceratops*, in all, a more powerful arrangement, possibly suggesting a wider gape. One highly aberrant species with respect to this feature is *Triceratops hatcheri*, in which the ventral squamosal flange is very short, so that the orientation of the *M. depressor mandibulae* approaches that of *Protoceratops* more closely than in any other ceratopsid.

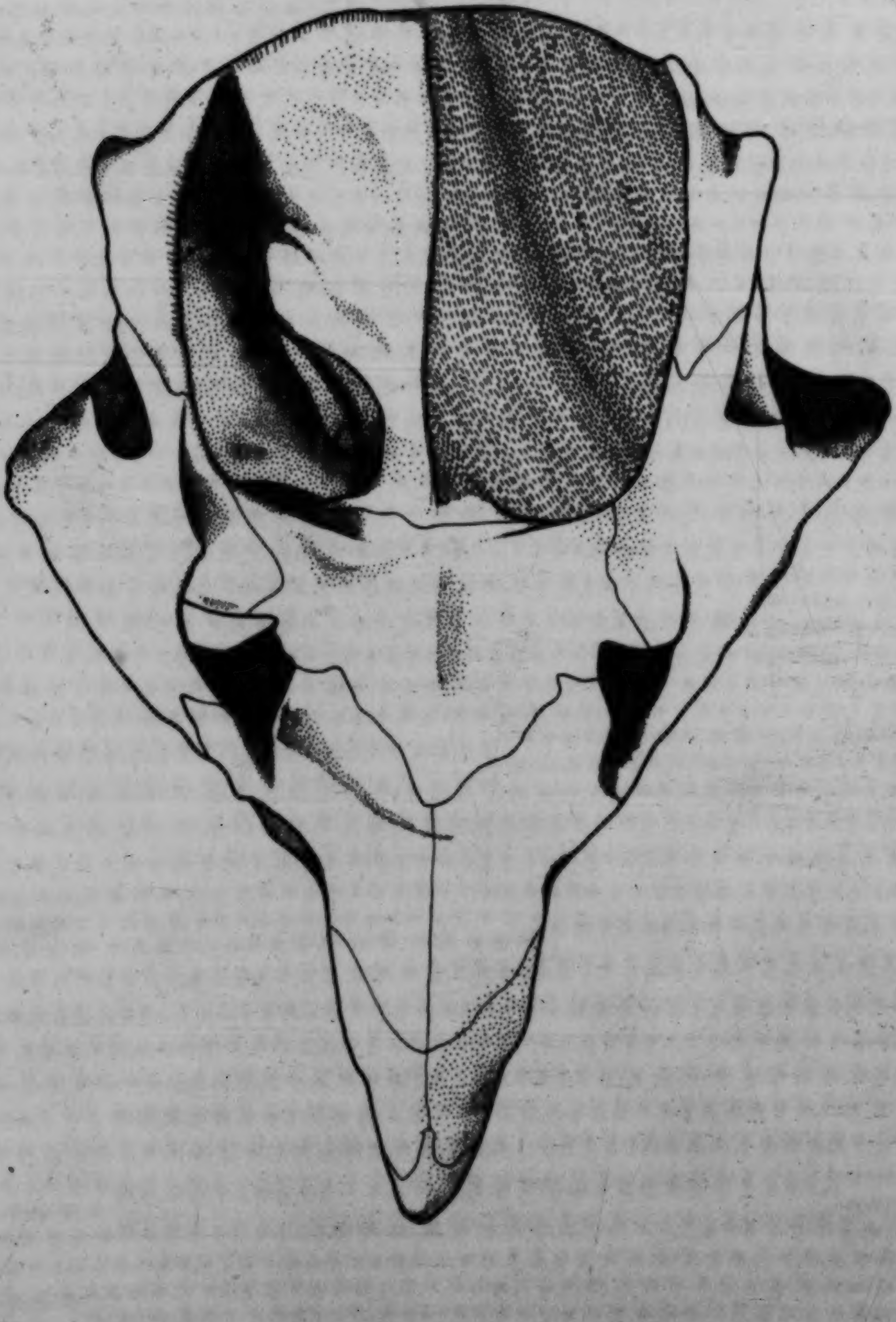
The *Mm. levator anguli oris*, *pseudotemporalis*, *levator bulbi*, *adductor mandibulae posterior* and *intermandibularis* probably were basically similar in all three families of the Ceratopsia. The other cranial muscles, however, show some variation between the families.

Haas (1955) has shown convincingly that there was a separate lateral portion of the *M. adductor mandibulae externus superficialis* in *Protoceratops* and *Psittacosaurus*. *Leptoceratops* has a similar excavation on the ventral surface of the jugal and so probably also had a separate lateral division of this muscle and similar conditions probably existed in other protoceratopsids and in *Protiguanodon*. All these forms are characterized by short skulls that are very broad across the jugals, and by low, broad coronoid processes with a distinct basal ridge, as described by Haas (1955) for *Protoceratops*. There is no evidence of this lateral division in any ceratopsid.

The main mass of the *pars superficialis* was relatively much larger in protoceratopsids and psittacosaurids than in ceratopsids. In both the Protoceratopsidae and the Psittacosauridae the lateral temporal fenestra is relatively much larger than in the Ceratopsidae, altering the proportions of the entire posterior part of the skull.

Kurzanov (1972) showed that the *pars medialis* and *pars profundus* of *Protoceratops* could not have covered the entire dorsal surface of the frill but the same is not true for all protoceratopsids. *Leptoceratops* has a short, non-fenestrated frill, showing no indication of secondary closure of a fenestra. The floor of the supratemporal fossa merges with the frill, which could be described as merely a short extension of this floor. Examination of the dorsal surface of the frill reveals distinct muscle scars along the mid-parietal crest and along the posterior border of the frill. The lateral edge of the supratemporal fossa shows deep striations as well. These scars likely mark the areas of attachment of a tough fascia that covered the *pars medialis* and *pars profundus* of the *M. adductor mandibulae externus*, which in turn covered the dorsal surface of the frill (Fig. 21). Striations on the more posterior part of the frill indicate that the posterior part of this muscle mass was tendinous (again, inserting tangentially on the bone surface and hence very strong) but the anterior part of the floor of the supratemporal fossa is smooth, indicating a broad, thick muscle passing antero-ventrally to insert on

Fig. 21. Dorsal view of right supratemporal fossa and postulated appearance and placement of fascia covering left supratemporal fossa of NMC 8889 (*Leptoceratops gracilis*), x.43. (From a photograph originally published by Sternberg (1951). Through the courtesy of Dr. D. A. Russell and the National Museums of Canada.)



the lower jaw.

Since specimens of *Leptoceratops* are not available in large numbers, as they are for *Protoceratops*, there could be considerable variation in the shape and orientation of the frill, but in all available specimens the contours of the frill are such that a muscle reaching the back of the frill would pass directly through the supratemporal fossa without any of the contortions neccessary for such an arrangement in older specimens of *Protoceratops*. As in the ceratopsids, there is no osteologic evidence of division into *medialis* and *profundus* masses and the muscle on the dorsal surface of the frill may have been undivided, although the size of the muscle mass argues against this interpretation.

Bagaceratops is a small protoceratopsid from Mongolia, recently described by Maryanska and Osmolska (1975). The frill is short and probably not fenestrated, although the preservation is not good enough to be certain on this point (Maryanska and Osmolska 1975). Maryanska and Osmolska's diagrams are not sufficiently detailed to show muscle scars but it appears that the *pars medialis* and *pars profundus* arose from the saggital crest, posterior border of the frill and lateral edge of the supratemporal fossa, as in *Leptoceratops*. The postero-lateral edges of the frill of *Bagaceratops* flare laterally, rather than being rounded as in *Leptoceratops*, but not to such a degree as to prevent a straight passage from the dorsal surface of the frill through the large supratemporal fossa.

Microceratops is the most primitive and geologically oldest protoceratopsid, although it cannot be regarded as an ancestor for the other protoceratopsids (Maryanska and Osmolska 1975). The frill in *Microceratops* is short with a rounded posterior border, as in *Leptoceratops*, but the frill is fenestrated, as in *Protoceratops*. The shape of the frill indicates that the *pars medialis* and *pars profundus* covered the entire dorsal surface of the frill, although in this case, the posterior part of the muscle mass overlay the frill fenestra. This situation, if correctly reconstructed, was restricted to *Microceratops* among all known ceratopsians. L. S. Russell (1935) suggested that the fenestrae in ceratopsid frills allowed bulging of the "*M. temporalis*" upon contraction but even if the adductor muscles had covered the dorsal surface of ceratopsid frills, it seems unlikely that the frill fenestrae would allow any more bulging than would the skin covering the muscle. Similarly, it is unlikely that the fenestrae in *Microceratops*, which were covered by musculature in life, functioned in this way. Possibly, their function was to lighten the frill, or they may have had some function unique to this genus.

Psittacosaurids also possess a short, non-fenestrated posterior extension of the parietals, although this platform is not nearly so extensive as the frill of ceratopsids or protoceratopsids. In these forms, the supratemporal fossa covers the entire dorsal surface of the platform, except for the short posterior extensions of the squamosals, and this platform functioned to support the *medialis* and *profundus* divisions of the *M. adductor mandibulae externus*.

In both protoceratopsids and psittacosaurids, the *pars medialis* and *pars profundus* probably inserted in the large inframandibular fossa rather than on the low, broad coronoid process. Correspondingly, in ceratopsids, the *pars medialis* and *pars profundus* inserted on the coronoid process and the *M. adductor mandibulae posterior* inserted in the inframandibular fossa, whereas the *M. adductor mandibulae posterior* of protoceratopsids and psittacosaurs probably inserted on a ridge medial to the fossa. In other respects, the *M. adductor mandibulae posterior* appears to have been very similar in all ceratopsians.

As mentioned above, the ectopterygoid of ceratopsids is very different from that of protoceratopsids, forming a rugose knob rather than a broad, sheathing element. This expanded knob provided a larger area of attachment that, together with the greater development of the retro-articular process, indicates a larger and more powerful *M. pterygomandibularis dorsalis*. The origin of the *pars ventralis*, on the other hand, appears to have been simplified with respect to the condition in protoceratopsids. (The skulls of psittacosarids are not known in sufficient detail to comment on their affinities in this regard.)

Neither protoceratopsids nor psittacosaurids possess the ventro-anterior squamosal flange that characterizes the ceratopsids. Hence, the *M. depressor mandibulae* must have arisen from the short, postero-lateral surface of the squamosal, giving this muscle a much more vertical orientation than in ceratopsids (with the possible exception of *Triceratops hatcheri*). This muscle, being both relatively longer and more vertical than in ceratopsids, would have produced a relatively greater torque around the jaw articulation than the *M. depressor mandibulae* of ceratopsids, although with respect to the adductor muscles, the *M. depressor mandibulae* of protoceratopsids and psittacosaurids still was relatively small.

Of the four groups of reptilian dorsal axial muscles, only three, the long median, long lateral and occipital groups have attachments on the skull (Olson 1936). The members of the long median group lie next to the vertebral column and slightly dorsal to the members of the long lateral group while the occipital group lies deep to the other two systems and consists of short muscles extending from the anterior cervical vertebrae to the atlas and occiput (Hyman 1942).

One of the most distinctive scars on the ceratopsid occiput consists of a pair of dorso-ventrally-elongate depressions, separated by a conspicuous ridge, lying dorsal to the foramen magnum. Lull (1908) felt that these depressions were the insertional areas for parts of the *M. longissimus dorsi* but since these scars occupy a median position in all ceratopsid skulls, it is unlikely that they were associated with the *M. longissimus dorsi*, which belongs to the lateral series of epaxial muscles (Hyman 1942; Olson 1936). L. S. Russell (1935, p.43) identified this area as "the common insertion area of the biventor cervicis ["*spino-occipitalis*"] muscles". According to him, there is a single depression in this area in *Chasmosaurus*, *Centrosaurus* and *Anchiceratops* but a pair of depressions in *Styracosaurus* and *Triceratops*. While it is true that the median ridge is more noticeable in some specimens than in others, there is always a pair of elongate depressions, separated by a ridge, in this area of the ceratopsid skull, even in NMC 2280 (*Chasmosaurus belli*), the specimen figured by Russell. The *M. biventor cervicis* also is a member of the *longissimus* system (Olson 1936) and thus seems an unlikely candidate for such a median position on the skull. In *Sphenodon*, modern lizards and crocodiles, the *M. spinalis capitis* "occupies a superficial position [on the occiput] very close to the midline" (Ostrom 1961, p.113). Such a position corresponds very well with the elongated scars above the foramen magnum of ceratopsids, which seem more likely to have received the *M. spinalis capitis* than any part of the lateral longissimus series. The median ridge dividing the two muscle scars very probably received a strong *ligamentum nuchae*. (Olson (1936) restored a similar condition in the cotylosaur *Diadectes* and the pelycosaur *Dimetrodon*.) Both the *M. spinalis capitis* and the *ligamentum nuchae* would arise from the neural spines of the cervical vertebrae and since their main function is to support the head (Lull and Wright 1942), it seems likely that both the muscle and the ligament were very strongly developed in ceratopsids. Indeed, the depth of the muscle scars and the height of the median ridge support this assumption. As in modern lacertilians (Olson 1936) and *Sphenodon* (Hyman 1942), the origin of the *M. spinalis capitis* probably consisted of separate tendons arising from the neural spines, but the smooth texture of the floor of the depressions on the occiput indicates a fleshy insertion. (A fleshy insertion also characterizes the attachment of the *M. spinalis capitis* of lacertilians (Olson 1936) and *Sphenodon* (Hyman 1942).)

There are two major muscle systems in the long lateral group of reptilian epaxial muscles: the *longissimus*, which occupies the entire length of the vertebral column, and the more lateral *ilio-costalis*, which does not always extend into the cervical region (Olson 1936). That part of the *longissimus* that occupies the cervical region is termed the *longissimus cervico-capitis* and can itself be divided into several muscles (Olson 1936). The most dorsal one, the *M. articulo-parietalis* (*complexus major*), can combine at its insertion with the *M. spinalis capitis* (Olson 1936). If this muscle was present in ceratopsids, it presumably had a similar combined insertion with the *M. spinalis capitis*, for it left no separate scar on the occiput. Of the other three divisions of the *M. longissimus cervico-capitis*, only the

Mm. *tranversalis cervicis* (*complexus minor*) and *capitis* (*spinalis colli*) have insertions on the skull. The *M*. *transversalis capitis* of *Iguana* inserts on the basioccipital (Olson 1936) and the basioccipital of ceratopsids has a deeply concave posterior face that presumably received this muscle. The *M*. *transversalis cervicis* of *Iguana* inserts more dorsally and more laterally on the occiput (Olson 1936). Lull (1908) showed a small, separate muscle scar on the basioccipital, directly above that here identified as the insertion of the *M*. *transversalis capitis* but I have not been able to distinguish such a scar in any ceratopsid. There is a deep scar below the ventromedial border of the exoccipital, however, that probably accomodated the *M*. *transversalis cervicis*.

The other part of the long lateral group of epaxial muscles that attaches to the occiput, the *M*. *ilio-costalis*, consists of two muscles: the *Mm*. *ilio-costalis cervicis* and *capitis* (Olson 1936). In *Iguana*, the *M*. *ilio-costalis capitis* inserts in common with the *M*. *transversalis capitis* (Olson 1936) and this probably was the situation in ceratopsids as well, since the area available on the posterior face of the basioccipital is large and there are no other suitable scars in this area. The *M*. *ilio-costalis cervicis* probably shared the insertional area of the *M*. *transversalis cervicis*, as again, there are no other suitable scars in this area.

The occipital group of reptilian epaxial muscles includes a medial M. rectus capitis and a lateral M. obliquus capitis, both of which usually are further subdivided (Olson 1936). Apart from the insertion of the M. spinalis capitis and the ligamentum nuchae, the most conspicuous scars on the ventral surface of the ceratopsid frill consist of two deep, oval depressions on the dorsal borders of the exoccipitals. Both Lull (1908) and L. S. Russell (1935) described these depressions as the areas of insertion of the M. rectus (capitis) posticus major. Lull (1908) divided the M. rectus capitis into four portions, with insertions on the basioccipital and beneath the ventromedial edge of the exoccipital as well, while L. S. Russell (1935) proposed two divisions, with the "anticus" portion inserting on the ventro-lateral edge of the exoccipital and the "posticus" portion inserting in the deep depression on the dorsal border of the exoccipital. Russell's reconstruction of the "anticus" portion is unlikely to be correct since, in modern reptiles, the M. rectus capitis anterior, along with the M. tranversalis cervicis, lowers or flexes the head (Ostrom 1961). Therefore, a lateral position for this muscle is unlikely. Lull's placement of the M. rectus capitis anterior with the M. tranversalis cervicis may be correct, as there are no separate scars for this portion. Although Lull divided the M. rectus capitis posterior, there is no clear evidence for this in ceratopsid skulls. The scar on the dorsal edge of the exoccipital is deep and probably received all the fibres of this muscle, although it is possible that a slip of the *M. rectus capitis posterior* inserted in common with the *M. transversalis capitis* and *M. ilio-costalis capitis*. In *Sphenodon* and modern lacertilians, the insertions of the *Mm. transversalis capitis* and *obliquus capitis magnus* are closely associated, and these two muscles have similar functions of rotation and abduction of the head (Ostrom 1961). In ceratopsids, it appears that the *M. obliquus capitis magnus* was much the stronger muscle as the area assigned to the *M. transversalis capitis* is small and close to the occipital condyle so that its moment arm would be small.

Lull (1908) figured a very large scar covering the lateral portion of the exoccipital and adjacent parts of the squamosal of *Triceratops*, labelling this scar as part of the insertional area of the *M. latissimus dorsi*. L. S. Russell (1935) labelled the exoccipital contribution of this area the "*rectus capitis anticus minor*" but, as mentioned above, the lateral position of this scar argues against such an interpretation. Although most ceratopsids have a shallow concavity on the ventral surface of the squamosal, this depression is separated from that on the exoccipital by a ridge on the lateral edge of the exoccipital, and often by a ridge on the squamosal as well. Further, this concavity appears to be too extensive and ill-defined to represent a muscle scar. The *M. complexus minor* (*tranversalis cervicis*) (Olson 1936) is a division of the *M. longissimus cervico-*

capitis, not of the *M. latissimus dorsi*, as stated by Lull (1908). It seems more likely that the *M. transversalis cervicis* would insert near the ventral surface of the braincase, as in *Sphenodon* and lacertilians (Ostrom 1961), rather than in the extreme lateral position postulated by Lull (1908). The function of the *M. obliquus capitis magnus* (rotation and abduction of the head) and its large size in most modern reptiles, where it is the largest muscle producing a lateral rotation of the head (Ostrom 1961) indicate that this muscle created the scar on the ventro-lateral surface of the exoccipital in all ceratopsids.

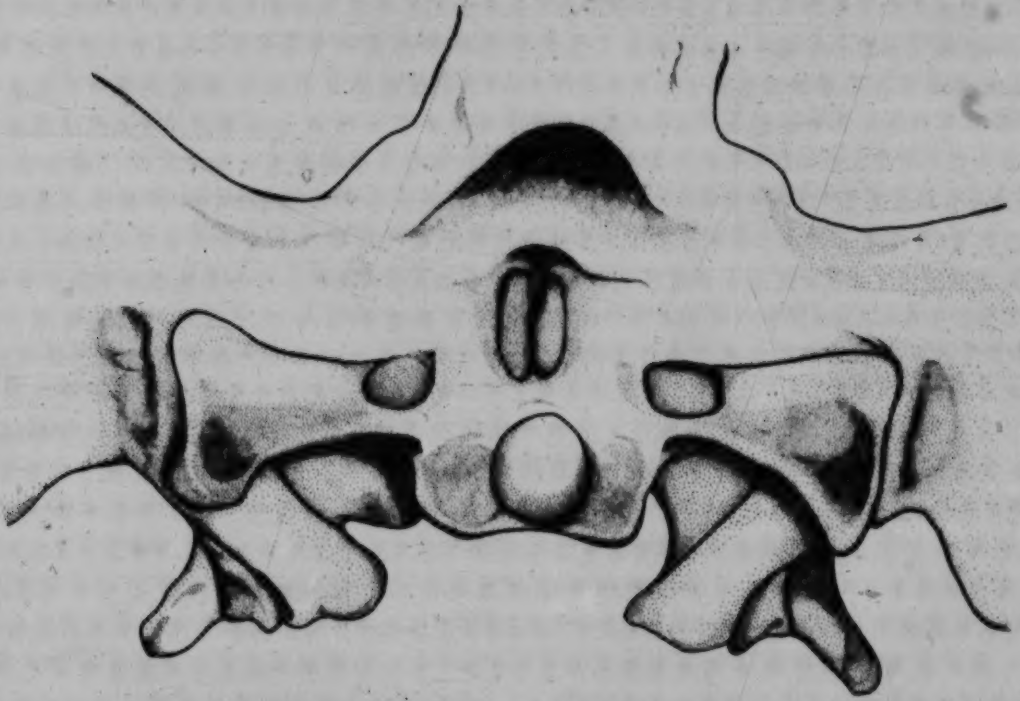
Of the hypaxial muscles, only the *M. subvertebralis* reached the occiput, attaching to the large rugose ventral surfaces of the basal tubera, immediately ventral to the insertions of the *Mm. transversalis cervicis* and *iliocostalis cervicis*.

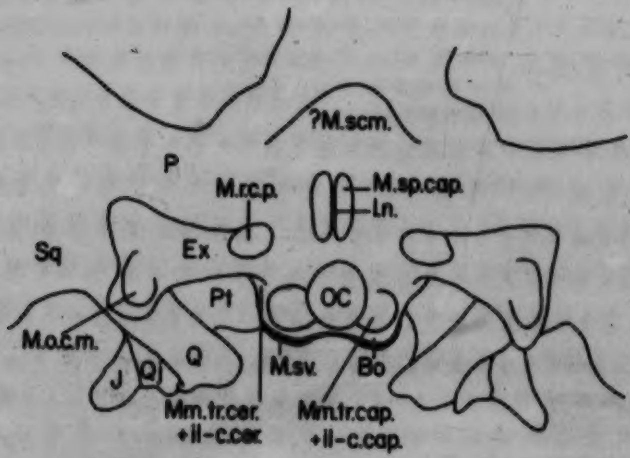
Lull (1908, pl. III) figured but did not describe an area on the ventral surface of the parietal, near the parieto-squamosal suture, which he labelled "?*levator claviculae*". This area, if it is indeed a muscle scar, is not strongly delimited from the rest of the ventral surface of the frill. I am unable to discern a distinct scar in this area in any ceratopsid and am inclined to believe, especially considering the extreme lateral position of this muscle on the parietal, that this area did not receive a muscle in the Ceratopsidae.

The only other prominent scar visible on the ventral surface of the frill in ceratopsids is a single median depression dorsal to the scars of the *M. spinalis capitis*. L. S. Russell (1935) identified this scar as the area of origin of the "capiti-dorsi-clavicularis" (trapezius) muscle. (L. S. Russell (1935) stated that Lull (1908) identified this scar as part of the insertion of the "*complexus*" but in fact, Lull's description refers to the dorsal extent of the *M. spinalis capitis* scars. Lull did not figure this separate, dorsal scar, although it is present in all ceratopsids.) Although this scar shows no indication of a division into left and right, as one might expect if it represents the origin of the trapezius group on both sides of the skull, it lies in the correct position to be the origin of part of the trapezius group, possibly a separate *M. sternocleidomastoideus*. This depression is the most dorsal scar on the frill. No other muscle appears to have attached more closely to the perimeter of the frill, so that most of the ventral surface of the parietal and all of the ventral surface of the squamosal were free of muscular attachments in life.

The arrangement of the muscles, or at least of the muscle scars, on the ventral surface of the frill was very constant among ceratopsids (Fig. 22). There are minor variations in the size and shape of certain attachments, many of which may be due to distortion rather than variation in shape or power of the muscles involved. In NMC 2280

Fig. 22. Areas of muscle attachment in the occiput and ventral frill surface of UA 11735 (Centrosaurus sp.).



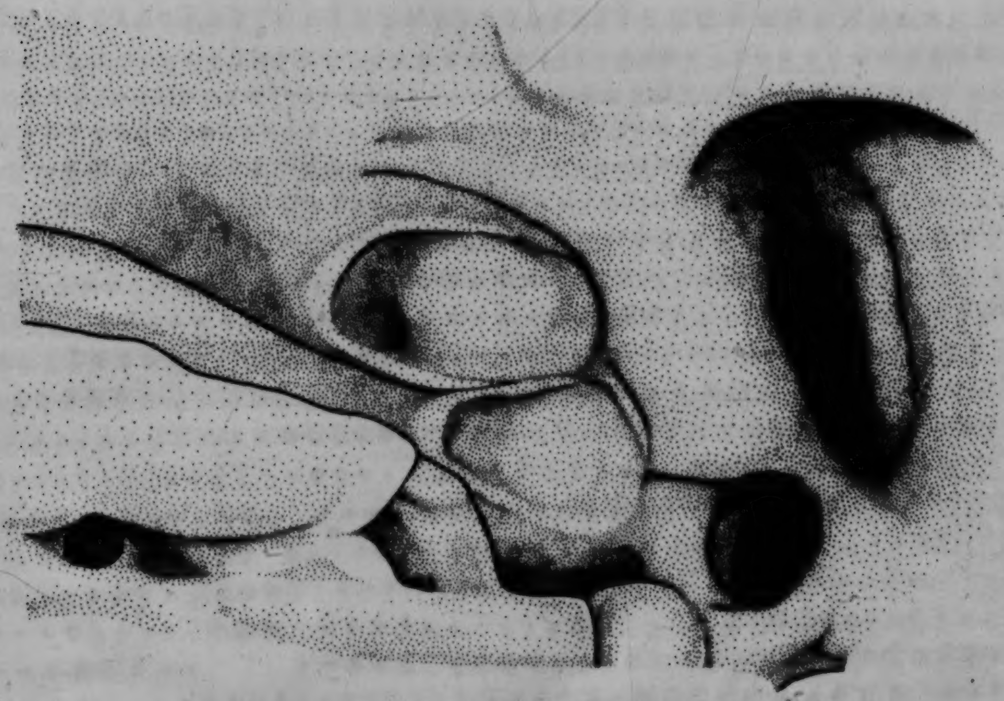

?M.scm.
P
M.r.c.p.
M.sp.cap.
l.n.
Sq
Ex
Pt
OC
M.o.c.m.
Q
J
Q
M.sv.
Bo
Mm.tr.cer.
+il-c.cer.
Mm.tr.cap.
+il-c.cap.

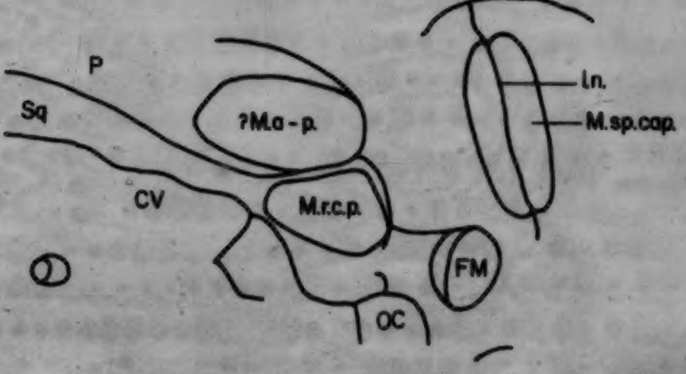
(*Chasmosaurus belli*), however, there is a large and very distinct muscle scar immediately dorsal to the area of insertion of the *M. rectus capitis posterior* (Fig. 23). L. S. Russell (1935) described this scar as the insertion of part of the *M. longissimus cervico-capitalis*. It is unlikely that either transversalis muscle had such a dorsal attachment (see above) but it is possible that the *M. articulo-parietalis* inserted in this area. Alternatively, this scar may represent a separate head of the *M. rectus capitis posterior*. Such a scar does not appear in any other specimen of *Chasmosaurus* nor, as far as I am aware, in any other ceratopsid.

The ventral surface of the frill of UA 40 (*Eoceratops*) is badly crushed and the surface is poorly preserved. Nonetheless, one can discern scars for the *M. spinalis capitis* and *ligamentum nuchae*, and for the *Mm. rectus capitis posterior*, *transversalis* and *ilio-costalis capitis*, *transversalis* and *ilio-costalis cervicis* and *obliquus capitis magnus*. Since the occiput of UA 40 is badly damaged and since the pattern of the muscles in this area is so constant in ceratopsids, the areas of muscular attachment are shown for UA 11735 (*Centrosaurus* sp.) (Fig. 22), which has a very well preserved occiput.

Protoceratopsids have muscle scars on the occiput that are essentially similar to those seen in ceratopsids, despite the different proportions of the elements forming the occiput. In *Protoceratops*, however, the exoccipitals

Fig. 23. Areas of muscle attachment on the occiput of NMC 2280 (*Chasmosaurus belli*). (Note separate scar for the *M. articulo-parietalis*.)



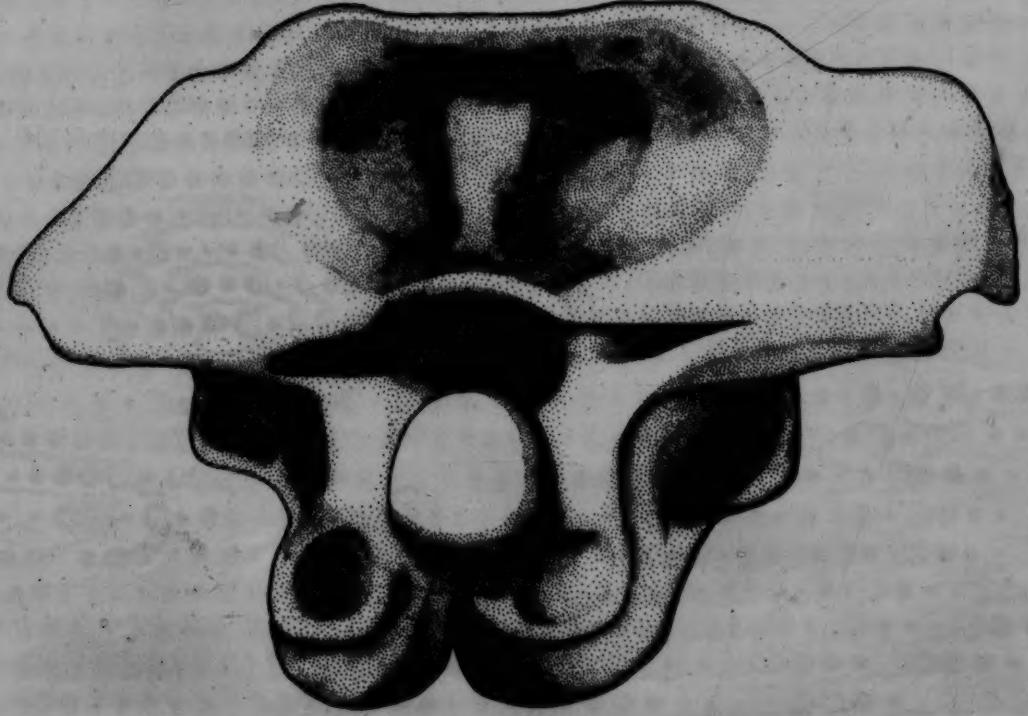

P
Sq
?M.a - p.
CV
M.r.c.p.
FM
OC
l.n.
M.sp.cap.

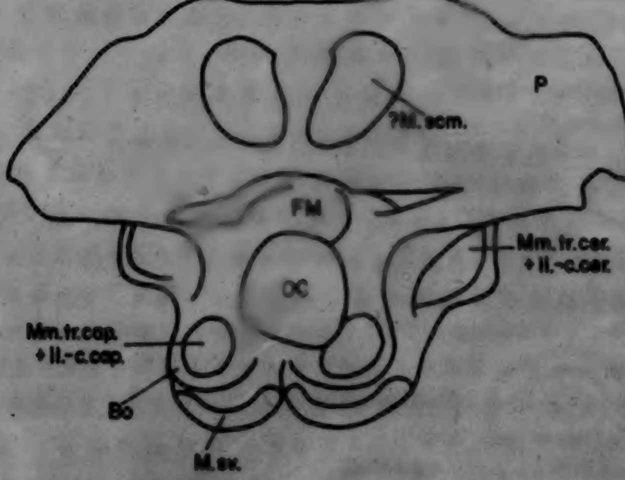
being relatively much longer than in ceratopsids, the area of insertion of the M. obliquus capitis magnus is in a much more lateral position. Leptoceratops also is fairly similar, although it appears to lack the deep depression for the M. sternocleidomastoideus seen in ceratopsids. The trapezius group presumably inserted somewhere on the ventral surface of the frill, possibly as far back as the posterior edge of the frill, the ventral surface of which is marked with parallel striations, as on the dorsal surface, although, more probably, these scars represent a slight ventral continuation of the fascia covering the dorsal surface of the frill. (The frill of Leptoceratops is much more restricted than that of Protoceratops so that a muscle attaching near the posterior edge of the frill would still be relatively close to the occipital condyle.) In Protoceratops, the exoccipitals lie essentially in a straight line, bracing the ventro-lateral sides of the frill. In some specimens of Leptoceratops, the two exoccipitals form an obtuse angle with each other, so that they brace the postero-lateral corners of the frill. This change in orientation places the insertional areas of the M. rectus capitis posterior very close to those of the M. spinalis capitis but otherwise, these scars are very similar to those seen in ceratopsids. (NMC 8887 (Leptoceratops) has its exoccipitals oriented approximately as in Protoceratops (Sternberg 1951).) The ventro-lateral surface of the exoccipital, however, shows no concavity for the reception of the *M. obliquus capitis magnus* and it is possible that this muscle occupied a more medial position than in *Protoceratops* and the ceratopsids, although there are no osteologic features to indicate the precise position of this muscle.

The descriptions of *Bagaceratops* and *Microceratops* available in the literature are not sufficiently detailed to indicate areas of muscular insertion on the occiput although the occiput of *Bagaceratops* is so similar to that of other protoceratopsids that the muscles inserting on the occiput probably were similar, as well.

In psittacosaurids, the muscles inserting on the ventral portion of the occiput appear to have resembled those of other ceratopsians. Dorsally, however, the occiput is very different from that of other ceratopsians, presumably at least in part reflecting a difference in the muscles inserting on this area (Fig. 24). The ventral surface of the parietal of AMNH 6254 (*Psittacosaurus mongoliensis*) is deeply concave. The dorsal rim of this concavity forms the posterior edge of the frill; the ventral rim forms a sharp ridge, which overlies the exoccipitals. Between this ventral ridge and the dorsal edge of the exoccipitals, there is a deep, open suture. Possibly, the medial surfaces of this ridge-suture complex received the *M. rectus capitis posterior*, and the *M. articulo-parietalis*, if such a muscle was present, while the lateral surfaces received the *M. obliquus capitis magnus*. There is a slight

Fig. 24. Areas of muscle attachment on the occiput of AMNH 6354 (*Psittacosaurus mongoliensis*). (Only part of skull shown.)




P
?M. scm.
FM
Mm. tr.cer. + Il.-c.cer.
OC
Mm.tr.cap. + Il.-c.cap.
Bo
M.ex.

depression on the dorso-medial surface of the exoccipital that probably indicates the area of insertion of the *M. rectus capitis posterior* but there are no features indicating the exact area of insertion of the *M. obliquus capitis magnus*.

The most obvious difference between the parietal of *Psittacosaurus* and that of other ceratopsians concerns the possible area of origin of the *M. sternocleidomastoideus*. Unlike the depression on the ventral surface of the frill in ceratopsids and *Protoceratops*, the concavity on the ventral surface of the parietal of *Psittacosaurus* is divided distinctly into left and right portions. If this concavity does indeed represent the attachment of the *M. sternocleidomastoideus*, this was the largest muscle attaching to the occiput of *Psittacosaurus*, as this depression is relatively much larger than in any other ceratopsian. (The parietal of AMNH 6253 (*Protiguanodon*) is incomplete but Osborn (1924, fig. 6) illustrated this element and there is a depression in the same (relative) position as the right *M. sternocleidomastoideus* scar in *Psittacosaurus*. Probably this area was similar to that in *Psittacosaurus*, although the rest of the area of origin of the *M. sternocleidomastoideus* is unknown in *Protiguanodon*.) Presumably, the *M. spinalis capitis* inserted on the raised, median area that separates the two ?*M. sternocleidomastoideus* depressions but the lack of a distinct ridge indicates that a *ligamentum nuchae* may not have been present in Psittacosaurus.

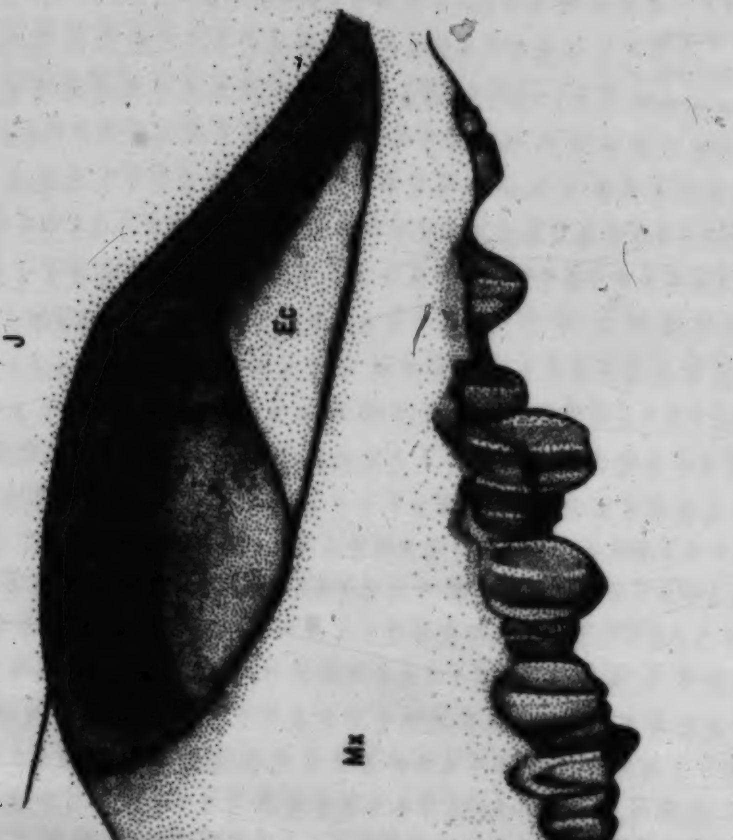
(b) Dentition

The restored cranial musculature of ceratopsids indicates a powerful jaw action, an assumption that is corroborated by the dentition, which shows adaptations for responding to heavy, rapid wear.

In his original description, Lambe (1902) assigned a separate tooth and a maxillary with teeth to Monoclonius (=Eoceratops) canadensis but, as mentioned previously, both of these specimens must be considered indeterminate. The left dentary (NMC 1254e) of NMC 1254 (Eoceratops) lacks teeth and the maxillary of NMC 1254 is not preserved, so other than a broken tooth in the left dentary of UA 40, the only known parts of the dentition of Eoceratops occur in the left maxillary of UA 40 (Fig. 25).

Except for a short, anterior, edentulous portion, the ventral border of the maxillary of UA 40 contains closely-spaced alveoli back to the incomplete posterior edge. There appear to have been approximately twenty-four tooth positions in the complete maxillary row. As in all ceratopsids, each maxillary tooth has a strongly developed longitudinal ridge on the posterior half of its labial surface. There are similar anterior and posterior ridges but, in unworn teeth, these do not continue to the tip of the crown, whereas the center ridge does. The edge of the

Fig. 25. Left lateral view of preserved portions of maxillary dentition of UA 40 (*Eoceratops canadensis*), x1.


J
Ec
Mx

crown, between anterior and posterior ridges, is marked by small crenulations. Although the edges of the maxillary teeth taper somewhat, the unworn coronal edge is rounded but there appears to be some variation among ceratopsids in this respect. The unworn dentary teeth of YPM 1821 (Triceratops flabellatus) are sharply pointed (see Hatcher, Marsh and Lull 1907, fig. 44), whereas the unworn maxillary teeth of YPM 1823 (T. serratus) (see Hatcher, Marsh and Lull 1907, fig. 42) are somewhat more rounded, although not as rounded as those of UA 40.

There is a thick, median ridge on the lingual surface of the maxillary teeth of UA 40, above the lingual root. Although the alveoli are smaller anteriorly, it is not possible to map differences in size along the tooth row, since many of the anterior teeth are missing. Where preserved, the fully erupted teeth are approximately the same size throughout the tooth row.

None of the teeth preserved in UA 40 shows the vertical shearing surfaces so characteristic of ceratopsids, those parts of the tooth series that participated in the occlusal surface having been lost.

As the tooth rows of UA 40 are incomplete, and no cross sections have been made of the jaws, it is not possible to describe the entire dental battery of Eoceratops. As far as is known, however, the general dental pattern is similar in all ceratopsids, so presumably Eoceratops followed this pattern as well.

Ceratopsid teeth do not form extensive dental batteries, as in hadrosaurs, although a large, continuous occlusal surface is formed in both groups. Unlike the hadrosaurian batteries, in ceratopsids, generally only one tooth in each vertical series is fully functional at one time (Ostrom 1964a), although other teeth may participate in the occlusal surface during replacement of older teeth. Within the family Ceratopsidae, the number of vertical series of teeth varies from twenty in Brachyceratops to forty in Triceratops (Ostrom 1966; Gilmore 1914) but according to Brown and Schlaikjer (1940c), ceratopsids are characterized by larger numbers of maxillary than dentary teeth. (In Triceratops, for instance, there may be at least ten more maxillary than dentary tooth positions (Brown and Schlaikjer 1940c).) Thus, when stating the maximum number of tooth positions in ceratopsids, presumably most authors are referring to the maxillary dentition. Further, while the number of tooth rows appears to have taxonomic significance, this number increases with age in Protoceratops and may do so in ceratopsids, as well (Ostrom 1966; Hatcher, Marsh and Lull 1907) so a range, rather than a single number should be used in the definition of a genus or species. The number of teeth in each vertical series depends upon the position of that series in the tooth row. Near the center of the row there can be four or five teeth per series (Ostrom 1964a), while at either end there can be only one (Hatcher, Marsh and Lull 1907) or two (Ostrom 1964a).

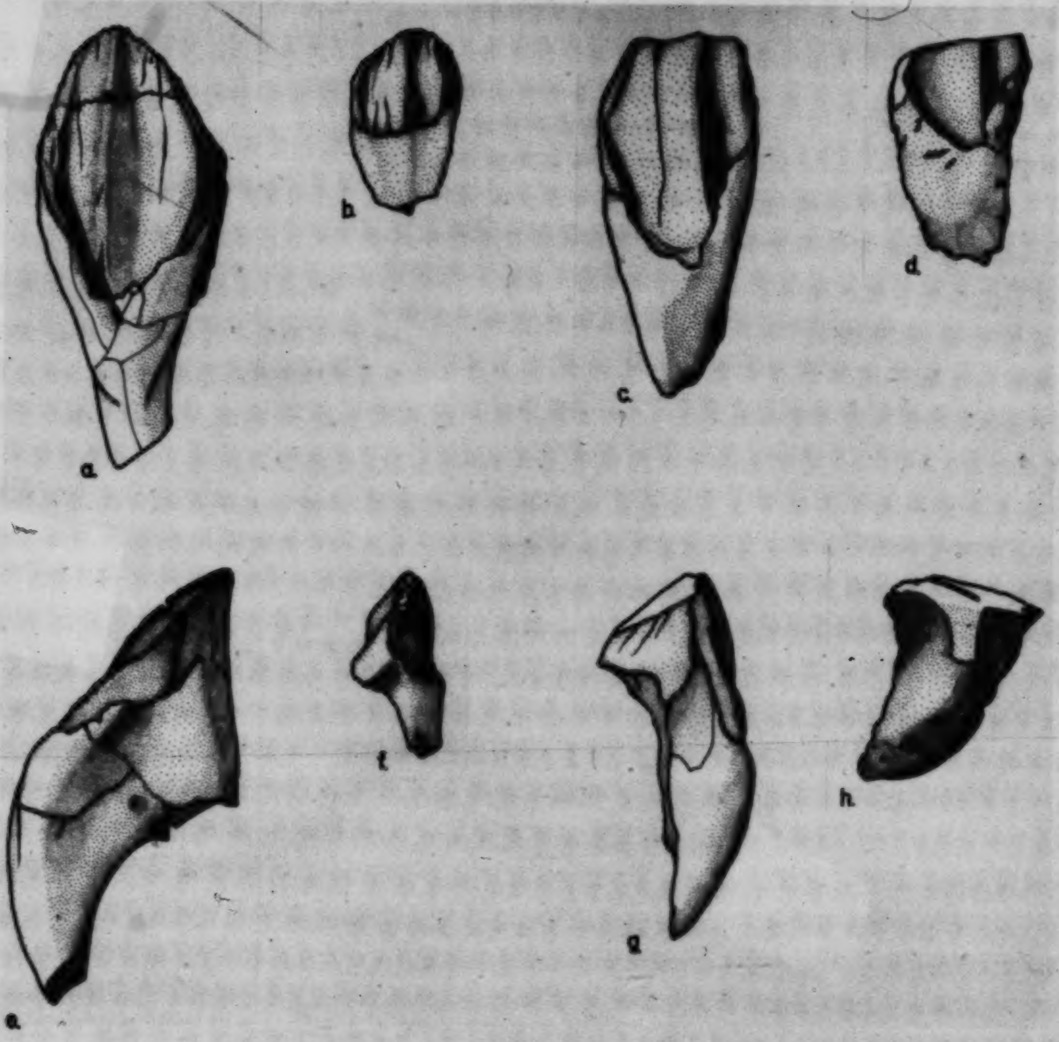
Ceratopsid teeth are unusual in that the tooth at the base of the vertical series has one large, triangular root, while older teeth in the same series have two roots. The double-rooted condition arises as the crown of the developing tooth presses into the pulp cavity of the next tooth in the same vertical series, the single root of which bifurcates to accommodate this crown (see Hatcher, Marsh and Lull 1907, figs. 43 and 45). Thus, each tooth is guided into its occlusal position by neighbouring teeth and by the succeeding tooth in the same series (Hatcher, Marsh and Lull 1907). On each side of a tooth, between the two roots, there is a groove, which facilitates close union with adjacent teeth and, as the tooth series in ceratopsids tend to be more or less strictly alternating (Ostrom 1964a; Edmund 1960), the crowns of the two neighbouring teeth are approximately on the same level below the edge of the intervening crown, so that a tight fit is maintained throughout the tooth row.

Ceratopsid teeth are strongly curved, convex on the lingual side, slightly concave on the labial side in the dentary series, with this orientation being reversed in the maxillary series. The vertical tooth series are curved as well, continuing the curve of the individual teeth, with the root on the convex side fitting into a ledge on the succeeding tooth, so that the whole dental battery is strongly interlocked. (See Hatcher, Marsh and Lull 1907, fig. 43.) As with the individual teeth, the maxillary tooth series curves in the opposite direction to the dentary series. Due to the curve of the teeth, the curve of the tooth series and the interlocking of each tooth with both neighbouring teeth and with the succeeding tooth in the same series, there is a rotation of individual teeth around the long axis of the jaw during the processes of growth, eruption and wear. For the unerupted teeth, this rotation is clearly visible in cross sections of the jaw (for example, Hatcher, Marsh and Lull 1907, fig. 43; Ostrom 1966, fig. 3) but the rotation apparently continues during the functional life of the tooth, so that the angle of the wear facet with respect to the long axis of the central ridge and to the base of the crown changes during use (Fig. 26), as the old tooth is continually pushed toward the occlusal plane and away from the jaw.

The convex surface of each tooth in ceratopsids generally is enamelled (Ostrom 1964a) and supports three strong, longitudinal ridges such as were described for Eoceratops. (On the dentary teeth, these ridges are on the lingual surface and the central ridge lies on the anterior half of the tooth.) The edge of the crown bears crenulations and sometimes the ridges do, as well, unlike the ridges in Eoceratops, which are smooth. The opposite surface, marked by the thick median ridge, lacks enamel (Ostrom 1964a).

When occluded, the maxillary teeth of ceratopsids lie lateral to the dentary teeth. This arrangement allows the functional teeth to shear past each other, forming vertical

Fig. 26. Functional series of isolated teeth illustrating the rotation of the occlusal plane in ceratopsids with respect to the base of the crown. a. and e., APM P67.8.5, x1.56 and 1.51, repectively; b. and f., APM P66.33.4, both x1.43; c. and g., APM P67.18.1, both x1.61; and d. and h., APM P64.5.199, x1.58 and 1.40, respectively.


a.
b.
c.
d.
e.
f.
g.
h.

wear surfaces capped with enamel. The crenulations on the edge of the crown quickly wear away but the enamelled ridges, especially the central one, form large crenulations along the tooth row (Ostrom 1964a). According to Galton (1973) both forms of crenulation would increase the sharpness of the edge of the occlusal surface, presumably by increasing the surface area of that edge, without increasing its thickness. Since only one side of the teeth carries enamel, and so abrades more slowly, and since the curve of the maxillary teeth is opposed by that of the dentary teeth, the edges of both tooth rows are continually sharpened with use, retaining a sharp edge throughout the life of an individual tooth, although the relative position of that edge changes through wear. The placement of the enamel and the pattern of wear insure that the cutting edge is formed by the most resistant part of the tooth (Ostrom 1964a).

In some specimens, such as AMNH 907 and YPM 1823 (Triceratops serratus) (Ostrom 1964a), the occlusal surfaces of both the maxillary and dentary tooth rows are vertical but many specimens show some oblique wear surfaces. Ostrom (1964a, p.6) attributed such oblique orientations to "post-mortem distortion and crushing" or to "minor" natural irregularities but Lull (1908) felt that the wear surfaces generally were vertical only in the anterior portions of the jaws, becoming oblique posteriorly. (A similar condition is seen in Leptoceratops (McKenna and Love 1970), although tooth function is somewhat different in this genus.) Also, in most ceratopsids, the functional teeth in one ramus lie in a single plane and according to Ostrom (1964a), any variation from a planar tooth row also is either a post-mortem effect or a "minor" natural irregularity. Certainly it is true that the major component of occlusal action in ceratopsids would have been vertical and that the occlusal surfaces in many cases are more or less planar. Nonetheless, variations in wear surfaces indicate variations in jaw action, especially, as Lull (1908) noted, in the posterior parts of the jaws. Considering that such variations are so widespread, they must be accounted for in analyzing the function of ceratopsid jaws.

As mentioned above, the relationship of the rostral and predentary would prevent any anterior motion of the lower jaw, at least at or near full occlusion, and according to Ostrom (1964a), the posterior inclination of the glenoid surface would prevent posterior motions of the lower jaw, but since the glenoid surface of ceratopsids forms an "obliquely transverse groove" (Ostrom 1964a, p.9), some lateral motion of the jaws may have been possible. Lull (1908) suggested that a certain amount of lateral motion could have occurred in the initial stages of adduction. Since ceratopsids had a scissors-like action in closing the jaws (see below), the posterior teeth would be in contact before the anterior teeth. Closer to full occlusion, the opposed vertical shear surfaces would prevent any lateral motion of the jaws but in the initial stages of occlusion, when only the posterior teeth were in contact, lateral motions would be possible, producing the oblique wear surfaces visible in so many specimens and accounting for the fact that such surfaces are more common in posterior than anterior teeth. More force could be generated at the most posterior teeth (see below) and it is possible that a certain amount of grinding was advantageous in this area but no ceratopsid developed wear surfaces indicating that lateral motions as extensive as those seen in some modern herbivores were possible.

An isolated ceratopsid tooth (APM P64.5.199) (Fig. 27) shows oblique, parallel striations on the wear surface, indicating that some anterior-posterior motion was possible as well. Such striations indicate tooth-on-tooth contact and they parallel the direction of jaw action that caused them (Greaves 1973). Unfortunately, there is no way to estimate the position of this isolated specimen in the tooth row, or even to tell from which jaw it came,[1] nor am I aware of such marks in other ceratopsid specimens. Nonetheless, the orientation of the striations is such that purely vertical, or even lateral motion could not have produced them. Thus, some anterior-posterior jaw action must have been possible

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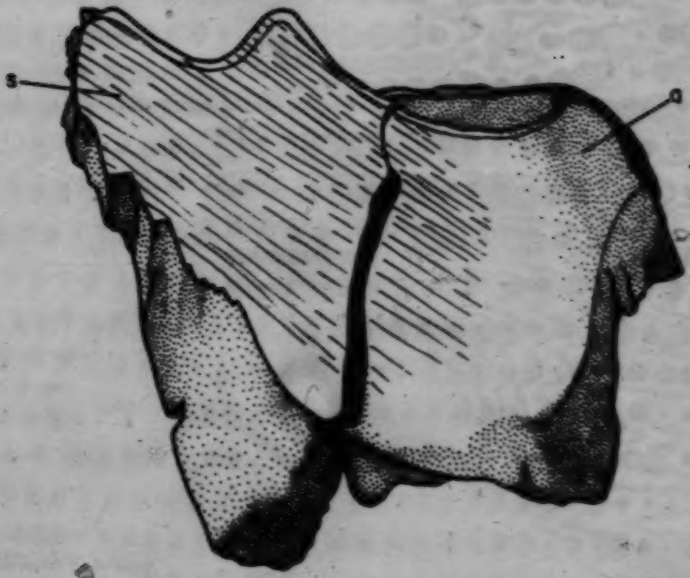
[1] Possibly, APM P64.5.199 is a maxillary tooth, since there is a slight ledge at the base of the central ridge (compare Fig. 26h with Hatcher, Marsh and Lull 1907, fig. 46) but since most of the roots of this specimen are missing and since the ledge in APM P64.5.199 is not as prominent as that figured by Hatcher, Marsh and Lull (1907) (although part of this difference could be taxonomic), this tooth cannot be assigned to a particular jaw ramus.

Fig. 27. Occlusal view of isolated ceratopsid tooth (APM P64.5.199) showing striations from tooth-on-tooth contact (s) and additional wear surface (a), x7. (See also Figs. 26d and h.)


s
a

in ceratopsids, at least in the individual that possessed this tooth. This specimen also shows an oblique wear surface that tapers away smoothly from the main wear surface. This oblique surface was formed by a tooth in the opposing ramus moving laterally and then proximally over the occlusal surface of this tooth. (The jaw action that produced the parallel striations could not have produced this oblique wear surface, as the long axis of the wear surface is approximately perpendicular to the striations.) The presence of both these features on a single tooth is strong evidence that jaw action in ceratopsids was not always a matter of simple vertical shear.

One of the features of the ceratopsid dentition that distinguishes it from the dentitions of protoceratopsids is the increased number of tooth positions and the extremely close spacing of these positions (Ostrom 1966). This close spacing, combined with the interlocking of adjacent teeth and the largely vertical wear surfaces produces a long, and in some cases essentially continuous occlusal surface, as in hadrosaurs. Unlike hadrosaur dentitions, however, the edge of the shearing surface in ceratopsids is irregular (Fig. 28). In hadrosaurs, the elongate roots are retained in the functional tooth row by interlocking neighbouring teeth, even after the crown is completely worn away (Edmund 1960), and the retention of heavily worn teeth ensures that the edge of the occlusal surface is more or less regular (Edmund 1960) (Fig. 29a, b). In ceratopsids, the teeth lie more or

Fig. 28. Medial view of right dentary of UA 41 (Centrosaurus sp.) showing irregular edge on shearing surface and bony masses (b) within vertical tooth rows.

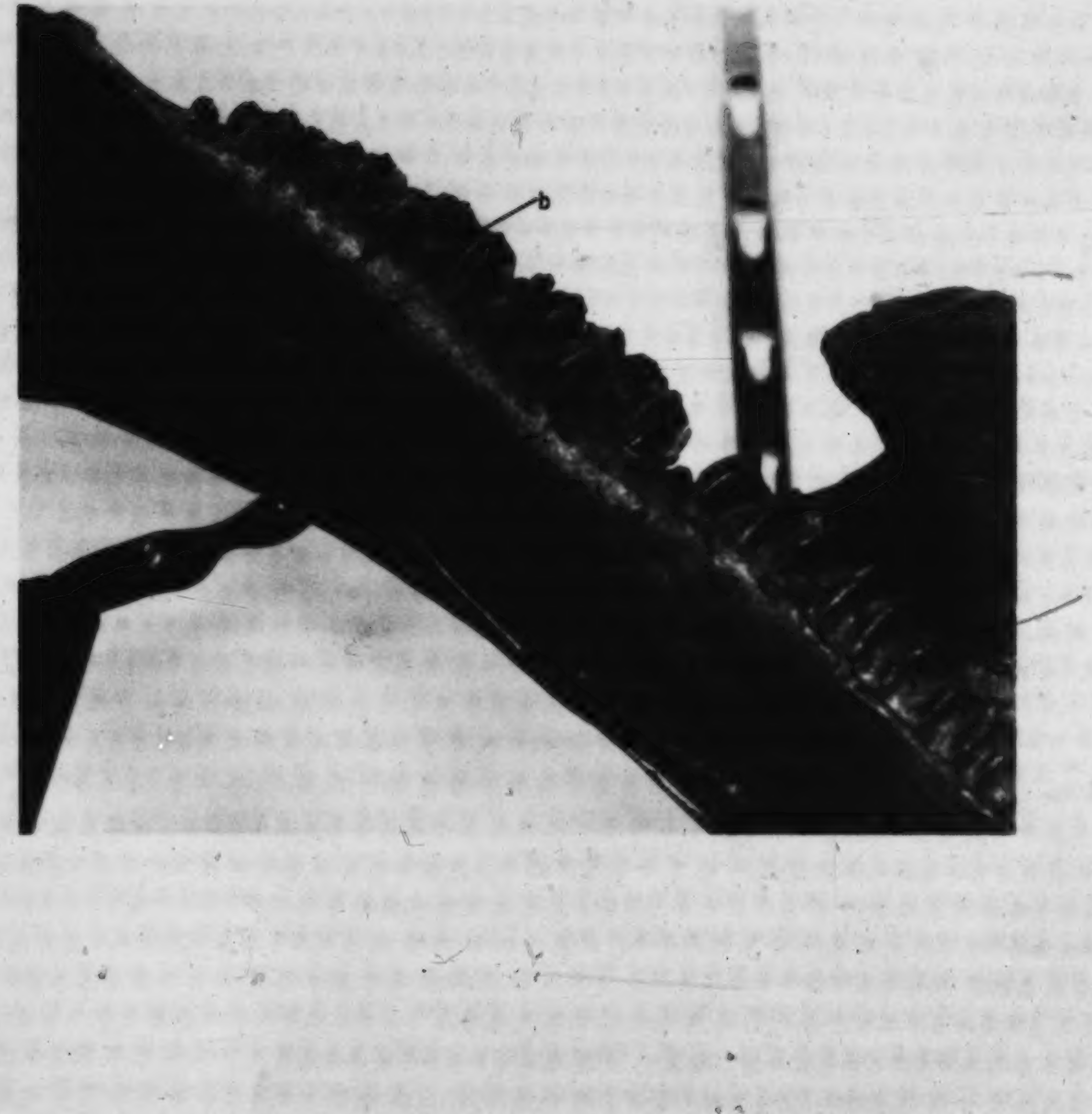
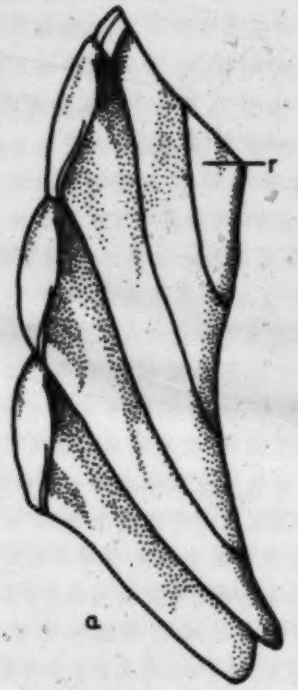
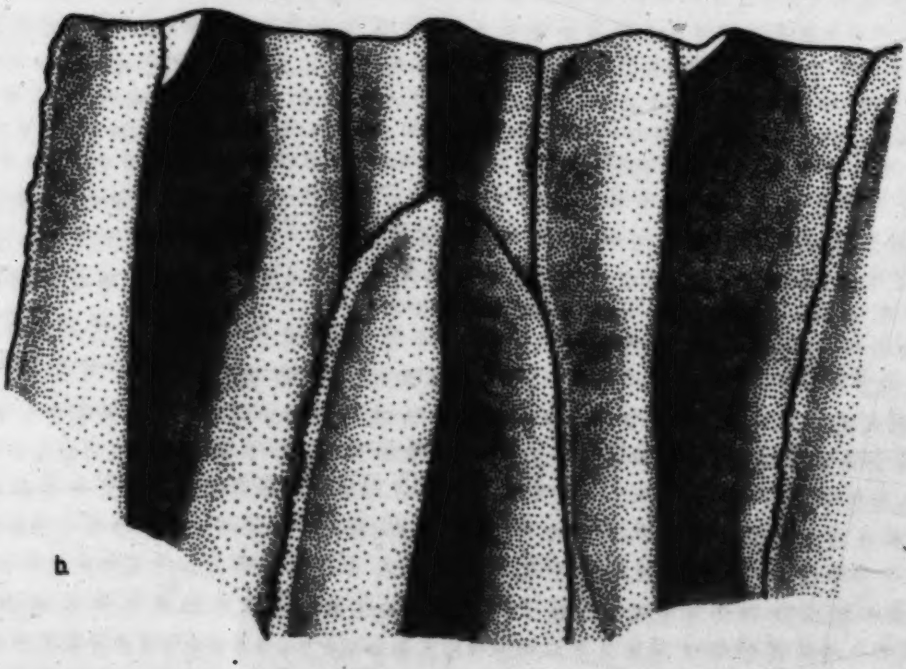

b

Fig. 29. a. ?Anterior view of a single vertical tooth series from the dentary of Anatosaurus anectens (from Lull and Wright 1940) showing retention of roots (r) even after crown is entirely worn away, x1.08. b. Lingual view of dentary teeth of an unidentified hadrosaur (UA 11734) showing even edge on occlusal surface, x3.4. (Compare with Fig. 28.)



a



b

less in vertical rows and despite the interlocking of adjacent teeth, the roots of heavily worn teeth are lost, at least in the fossil jaws, although in life they may have been held in place by connective tissue (Edmund 1960). Edmund (1960, p.152) described "small masses of bone overlying the junction of the crown of one tooth with the root of its predecessor" in the jaws of an unidentified Belly River (Judith River) ceratopsid (ROM 1944). These masses of bone may have helped to retain the roots of heavily worn teeth in the functional tooth row (Edmund 1960) but it is also possible that they served to further strengthen the dental battery, for even in jaws where such masses are common, the edge of the occlusal surface is highly irregular and roots are not retained (see Fig. 28). Although these bony masses are not mentioned elsewhere in the literature (Edmund 1960), they are quite common: Edmund reported their presence in AMNH 970 (*Triceratops serratus*), YPM 1834 (*T. brevicornus*), AMNH 5351 (*Centrosaurus nasicornus*), NMC 8800 (*Chasmosaurus russelli*) and AMNH 5402 (*C. belli*); they also are visible on UA 41 (*Centrosaurus* sp.) and NMC 285 (the right maxillary originally assigned to *Monoclonius* (=*Eoceratops*) *canadensis* (Lambe 1902) but here considered indeterminate). Further, Edmund (1960, p.152) stated that the dentition of YPM 1821 (*Triceratops flabellatus*) has "the tips of the roots broken away in every case, as if some persistant material, perhaps the bone described above, had been removed during preparation." (See also Hatcher, Marsh and Lull 1907, fig. 44.)

The teeth of protoceratopsids and psittacosaurids differ considerably from those of ceratopsids. In these two families there is always a major horizontal component in the occlusal action, either from the inclined occlusal surface or, in *Leptoceratops*, from a horizontal shelf on the dentary teeth. There are fewer teeth, ranging from six in immature specimens of *Bagaceratops* (Maryanska and Osmolska 1975) to seventeen in *Leptoceratops* (Ostrom 1966) and the teeth are smaller and not so closely spaced as in ceratopsids (Ostrom 1966). Both crowns and roots show less curvature, the central ridge is smaller and the tooth row is shorter and placed more anteriorly in the jaw, relative to the coronoid process (Ostrom 1966) (see below).

Protoceratops is unique among ceratopsians in the possession of premaxillary teeth. Both *P. andrewsi* (Brown and Schlaikjer 1940*c*) and *P. kozlowskii* (Maryanska and Osmolska 1975) have premaxillary teeth and Colbert (1948) stated that *Leptoceratops* also possesses premaxillary teeth but according to Sternberg (1951) and Ostrom (1966), the premaxillaries of *Leptoceratops* are edentulous. The premaxillary teeth of *Protoceratops* are small, peg-like structures, one pair on each side, posterior to the rostral (Ostrom 1966). Ostrom (1966) regarded the presence of premaxillary teeth in *Protoceratops* as a primitive feature but since such teeth are not found in psittacosaurids, which have a larger number of primitive characters than does

Protoceratops, and therefore may be regarded as lying closer to the common ancestor of ceratopsians, and since the premaxillary teeth of *Protoceratops* are simple structures, unlike any other teeth found within the Ceratopsia, and are not opposed by teeth in the mandible, it is possible that they are derived features, developed only in *Protoceratops*, from an ancestral ceratopsian with an edentulous premaxillary.

Protoceratops kozlowskii has seven maxillary teeth and seven dentary teeth in the smallest known specimens but may have as many as eleven in older individuals (Maryanska and Osmolska 1975) and *P. andrewsi* has thirteen to fifteen teeth in each jaw ramus (Ostrom 1966). The number of teeth increases with age in protoceratopsids but at any age, protoceratopsids have fewer teeth than do ceratopsids. The individual tooth positions are not as crowded as in ceratopsids but the teeth are relatively smaller so that the tooth rows are relatively much shorter and the ratio between the length of the dentary tooth row and the length of the mandible is considerably less than in ceratopsids (Ostrom 1966).

In form, the teeth of *Protoceratops* are rather similar to those of ceratopsids: the labial surface of the maxillary teeth and the lingual surface of the dentary teeth, are thickly coated with enamel and each of these surfaces supports a prominent ridge on the posterior half of the tooth in the maxillary row, the anterior half in the dentary row (Brown and Schlaikjer 1940c). The edge of the unworn crown is heavily crenulated, more so than in ceratopsids, and the central keel is relatively lower (Brown and Schlaikjer 1940c) but the method of eruption appears to have been basically similar to that inferred for ceratopsids: grooves on the anterior and posterior surfaces of the teeth admit the crowns of adjacent teeth, which, together with the succeeding tooth in the same tooth series would have pushed individual teeth into occlusal position (Brown and Schlaikjer 1940c). In *Protoceratops*, however, the root is single (Brown and Schlaikjer 1940c) and the curve of the teeth (Ostrom 1966), and hence of the vertical tooth series, is not so great. Coupled with the greater spacing of the teeth, these conditions produce a tooth row that is not so tightly interlocked as in ceratopsids. Further, there is only one replacement tooth at each tooth position (Ostrom 1966) or, at the most, two (Brown and Schlaikjer 1940c), indicating a slower rate of wear and eruption and possibly a relatively less abrasive diet than in ceratopsids. (The very different occlusal pattern of *Leptoceratops* (see below) also indicates a diet of highly resistant vegetation, however, or at least a diet unlike that of the Asian protoceratopsids.)

Despite the basic similarities, then, there are sufficient differences between the dentitions of *Protoceratops* and the ceratopsids to indicate very different jaw mechanics and the tooth wear surfaces support this interpretation. The occlusal surfaces in *Protoceratops* are oblique (Ostrom 1966), as in hadrosaurs, rather than vertical as in ceratopsids. According to Ostrom (1966), the oblique orientation of the occlusal plane in *Protoceratops* is related to the more nearly equivalent widths of the skull and lower jaws. Although the maxillary teeth bite outside those in the dentary, as in ceratopsids, in ceratopsids the maxillary teeth are relatively more laterally placed with respect to the dentary tooth row, allowing the two sets of teeth to shear completely past each other; this lateral shift presumably is correlated with the increased curvature of the vertical tooth series (Ostrom 1966), which affects the placement of the teeth upon eruption. Again, these differences probably reflect differences in diet, with a strong grinding component being important in the mastication of the preferred foods of protoceratopsids, whereas slicing movements were more important in ceratopsids.

The dentition of *Bagaceratops* is very similar to that of *Protoceratops*, both in structure and in patterns of wear (Maryanska and Osmolska 1975). According to Maryanska and Osmolska, the wear surfaces vary slightly along the tooth row but generally, in all protoceratopsids, the angle formed by the occlusal surface and the enamelled surface of the crown is greater in the maxillary than in the dentary teeth, with the exception of *Leptoceratops*, which has a unique dentition (see below). Thus, although the occlusal surface is oblique in both tooth rows, it is more nearly vertical, and more extensive, in the dentary teeth. The main difference between the dentitions of Bagaceratops and Protoceratops involves the greater development of the anterior and posterior ridges on the enamelled surface of the maxillary teeth of the latter (Maryanska and Osmolska 1975). The form of the labial surface of the posterior maxillary teeth changes with age in Bagaceratops, juveniles showing fewer crenulations and a lower central ridge that is more or less medial in position (Maryanska and Osmolska 1975).

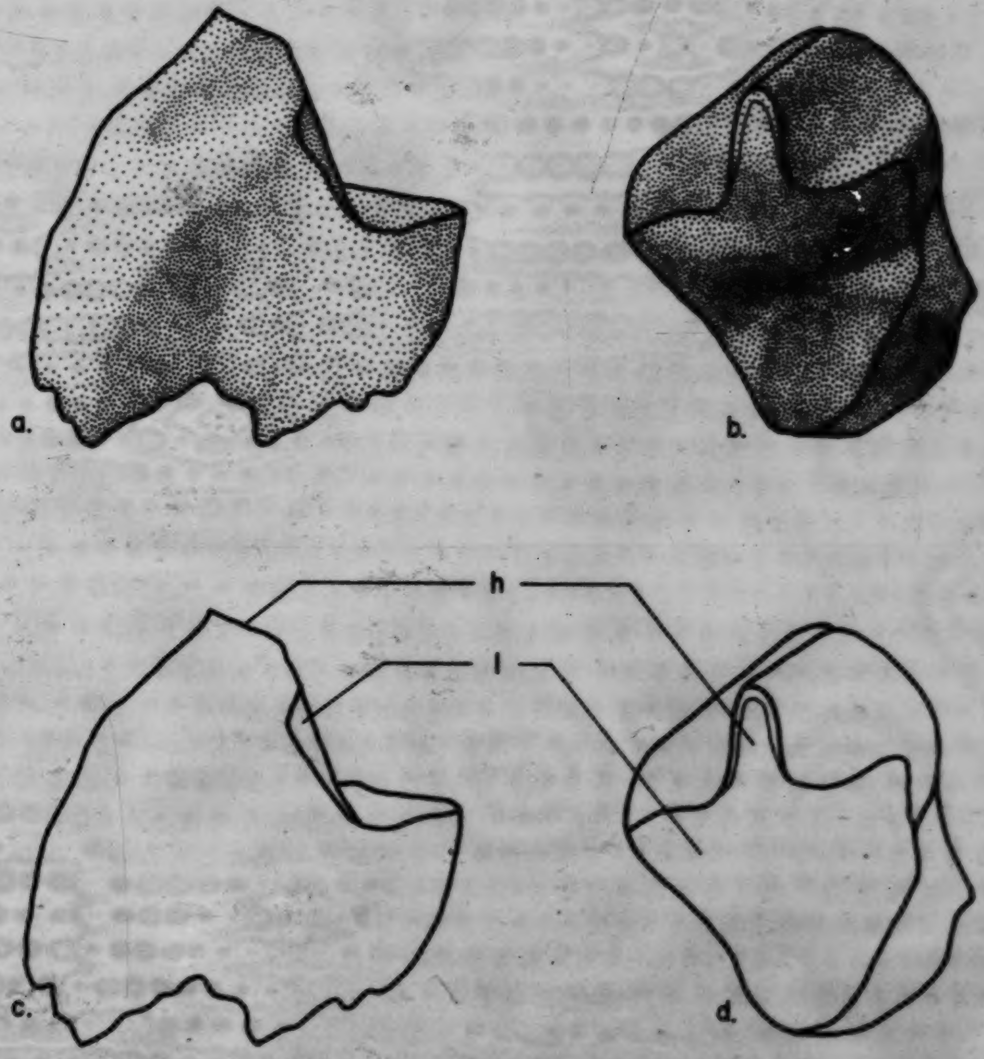
Perhaps the most striking characteristic of the dentition of Bagaceratops is the relative length of the anterior, edentulous portion of the maxillary, which, according to Maryanska and Osmolska (1975), accounts for 50% of the post-rostral jaw length. Ostrom (1966) stated that there was an increase in the relative length of the edentulous portion of the jaws in ceratopsids, with respect to that of protoceratopsids, but considering the large edentulous area in Bagaceratops, it appears that there was a relative increase in this character in certain protoceratopsids as well.

Although the basic structure of the teeth in Leptoceratops is similar to that in other protoceratopsids, the wear surfaces are very different, so that, among ceratopsians, the dentition of Leptoceratops is unique, implying a unique jaw action. The teeth of Leptoceratops are single-rooted (Brown 1914c) and there is a single functional tooth underlain by one replacement tooth (Ostrom 1966). On opposite surfaces in the upper and lower jaw, there is a thick layer of enamel, marked by prominent ridges (Brown 1914c). In the dentary teeth, there are two prominent wear surfaces, one vertical and one, on the labial surface, horizontal. In the maxillary teeth there is one, large vertical wear surface and a short horizontal surface on the end of the crown that occludes with the horizontal surface on the dentary teeth. Thus, the teeth of Leptoceratops performed both crushing and shearing functions. According to McKenna and Love (1970), the major wear surfaces of the posterior maxillary teeth are oblique, while more anteriorly, these surfaces are vertical, indicating a relatively complex action, and specimens of isolated teeth, both dentary and maxillary (PU 18133) (Fig. 30) (AMNH 2571, see McKenna and Love 1970, fig. 2A and B), show additional wear surfaces and striations on the "vertical" face, in more than one direction. McKenna and Love (1970) felt that the dental adaptations of Leptoceratops indicate a more varied diet than that of ceratopsids; certainly, they indicate a very different method of masticating food.

Montanoceratops, a protoceratopsid from the St. Mary River formation of Montana, "may have had teeth more like those of Leptoceratops" than those of Protoceratops (McKenna and Love 1970, p.D59), although this genus is still poorly known.

The teeth of psittacosaurids are rather different from those of other ceratopsians, being low-crowned and broad

Fig. 30. Isolated Leptoceratops tooth (PU 18133) from dentary, showing wear facets (h and l) additional to the horizontal and vertical facets characteristic of the teeth of this genus. a. and c., ?anterior view, x2.77. b. and d., occlusal view, x2.88. (Through the courtesy of Drs. J. H. Ostrom and D. Baird and Princeton University.)


a.
b.
h
l
c.
d.

antero-posteriorly (Osborn 1923, 1924), with enamel on both lingual and labial surfaces (Romer 1956). One can distinguish a basic pattern in psittacosaurid teeth that is shared with other ceratopsians, while the similarities with other ornithischians, particularly the iguanodontids, show clearly how the ceratopsian patterns were derived from other members of the Ornithischia.

Psittacosaurids have teeth only in the maxillary and dentary (Osborn 1923). The edentulous anterior portions of the jaws, plus the beak-like rostral and predentary bones immediately suggest ceratopsian affinities; but the individual teeth, exhibiting a large, central ridge and smaller anterior and posterior ridges oriented as in protoceratopsids and ceratopsids, with the ridges on the labial surface of the maxillary teeth (Osborn 1924) and lingual surface of the dentary teeth (Osborn 1923), also suggest a close relationship with ceratopsians. There are seven maxillary teeth in situ in AMNH 6261 (Psittacosaurus mongoliensis), which show that the central ridge lies on the posterior half of the labial surface (Osborn 1924), as in protoceratopsids and ceratopsids. In Protiguanodon, the central ridge divides both the labial surface of the maxillary (Osborn 1924) and the lingual surface of the dentary teeth (see Osborn 1923, fig. 4B) into equal halves. In both genera, these ridges are relatively more robust than in protoceratopsids and ceratopsids but they produce similar crenulations along the tooth row (Osborn 1924). The maximum number of teeth in the maxillary of Psittacosaurus is eight and in the dentary, nine (Young 1958) but there are not enough specimens known to tell if the number of teeth increased with age in psittacosaurids, as it does in Protoceratops. In Protiguanodon, there are nine dentary teeth (Osborn 1924) but the maxillary tooth row is known only from isolated teeth.

Psittacosaurids also share certain features with protoceratopsids that are not seen in ceratopsids. The tooth row ends opposite the anterior end of the coronoid process, the individual teeth are single-rooted (see Osborn 1923, fig. 5) and the wear surfaces on the individual teeth are oblique. Compared to protoceratopsid teeth, those of psittacosaurids are low, with rounded crowns that are relatively more robust in a lingual-labial direction and only a single functional and a single replacement tooth at each tooth position (Edmund 1960).

Maryanska and Osmolska (1975) included the family Psittacosauridae in the Suborder Ceratopsia, based partially on the similarity in tooth structure, and this assignment is accepted here.[1]

[1] "The skull of the psittacosaurids exhibits some attributes which are not present within any other group of ornithopods but are common to both the Protoceratopsidae and Ceratopsidae" (Maryanska and Osmolska 1975, pp.171-172). In addition to the similar tooth structure, these include: the presence of a nasal horn core (or incipient horn core) (in Psittacosaurus youngi); the presence of a frill, or an expanded parietal area for muscle insertion; increased skull width across the jugals; and the development of a rostral (see below) (Maryanska and Osmolska 1975).

(c) Mandibular mechanics

Having examined both the dentition and the possible arrangement of the jaw muscles, it should be possible to analyze the action of the jaws in the three families of ceratopsians.

One of the most characteristic features of the ceratopsian skull is the beak-like development of the anterior region of the jaws. All ceratopsians possess unpaired, median rostral and predentary bones that lack teeth. Osborn (1923) originally identified the anterior, beak-like bone in the upper jaw of Psittacosaurus as the premaxillary but Maryanska and Osmolska (1975) have argued convincingly that this element actually is the rostral. According to Maryanska and Osmolska (1975, p.172): "the bone identified as the 'premaxilla' is very small and it is far from the external nares. This relation is so unique [sic] among reptiles that it is difficult to believe such a structure could be found on a reptilian snout. More probably, the 'premaxilla' represents in fact the rostral", especially since this bone is not paired. "The unusually dorsally expanded 'maxilla' [therefore] includes the premaxilla although the suture between these bones has been obliterated" (Maryanska and Osmolska 1975, p.172). If this interpretation is correct, the anterior region of the jaws is basically similar throughout the Ceratopsia.

The rostral in all ceratopsians has a single dorsal projection, two posteroventral projections, lying lateral to the anterior extensions of the premaxillaries, and two sharp, concave ventral margins, meeting anteriorly in a sharp point. Often the rostral is fused to the underlying premaxillaries but in some cases, as in USNM 2116 (*Triceratops elatus*), it is disarticulated and shows a median septum on the posterior surface of the dorsal projection (see Hatcher, Marsh and Lull 1907, fig. 30). In life, this septum would have produced a strong, immobile union between the rostral and the premaxillaries. In addition, the lateral edges of the dorsal projection overlap the premaxillaries (Hatcher, Marsh and Lull 1907), so that this articulation is very strongly reinforced.

Although this basic pattern is present in all ceratopsians, there are some noticeable variations in the development of the rostral within each of the families and in some cases, even within single genera. In ceratopsids, although there is a great deal of variation in the rostral, it is possible to define three structural types with respect to the size and shape of the rostral and adjacent parts of the premaxillary. In *Triceratops flabellatus*, and probably in all species of *Triceratops* (although the rostral and premaxillaries often are thoroughly coössified), the rostral is relatively large, with a long dorsal process and a strongly curved posterior border, conforming to the anterior curve of the premaxillaries (Fig. 31a). In these forms, the large rostral is associated with a premaxillary that has a

Fig. 31. Right lateral view of rostral and premaxillary flange of a. YPM 1821 (Triceratops flabellatus) and b. AMNH 1624 (Pentaceratops sp.).

a.

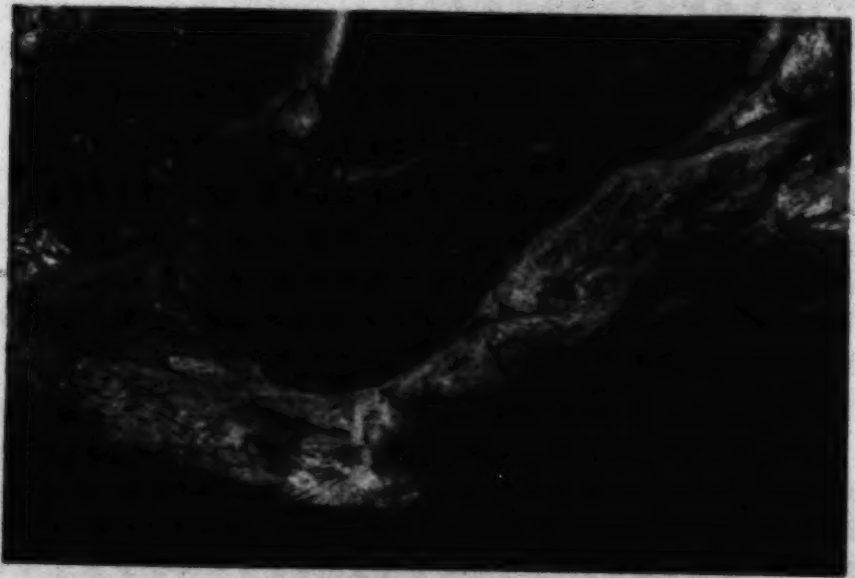
b.

relatively long ventral border that may be either more or less straight, or gently curved. In *Chasmosaurus belli*, *C. kaiseni*, *Pentaceratops* (Fig. 31b) and *Anchiceratops*, the ventral edge of the premaxillary is similar to that of *Triceratops* but the rostral is a small element, restricted to the very anterior end of the premaxillaries. The dorsal process of the rostral in these forms is short but the posterior edge of this element is strongly curved, as in *Triceratops*. In *Centrosaurus*, the rostral is a moderately large, triangular element with a short dorsal projection and a fairly straight posterior edge confined to the anterior tip of the snout. The ventral edge of the premaxillary is entirely unlike that of other genera, being relatively very short, with a strong ventral projection below the center of the external narial opening (Fig. 32a). (The rostral is unknown in *Styracosaurus* but the configuration of the premaxillary indicates that the rostral probably was very similar to that of *Centrosaurus*. *Pachyrhinosaurus* also has a narial region that is very similar to that of *Centrosaurus*, although the rostral is always so thoroughly coössified with the premaxillary that its extent cannot be determined.) *Arrhinoceratops* falls somewhere between the last two categories, having a fairly strong ventral projection on the edge of the premaxillary (Fig. 32b) and, seemingly, a small rostral confined to the anterior tip of the snout.

There is much less variation in the ceratopsid predentary, which is a basically triangular element with two

Fig. 32. a. Right lateral view of rostral and premaxillary flange of ROM 4519 (*Centrosaurus apertus*). b. Left lateral view of premaxillary flange of ROM 5135 (*Arrhinoceratops brachyops*).

a.



b.

postero-dorsal projections, embracing the dentaries laterally, and a complex postero-ventral projection that interdigitates with the antero-ventral edges of the dentaries. The main variation in the predentary concerns the dorsal edges, which converge anteriorly to form a sharp point. As far as is known, in all ceratopsids the dorsal edges of the predentary form, on each side, two longitudinal ridges with a shallow intervening trough. Except in Centrosaurus, both of these ridges are more or less horizontal, although anteriorly they curve dorsally to converge at the tip of the predentary. In Centrosaurus, the lateral ridge lies ventral to the level of the medial ridge, so that the intervening trough faces dorso-laterally. Since the other features of the jaws of Styracosaurus are very similar to those of Centrosaurus, it is possible that the predentary was similar as well but so far, the complete predentary of Styracosaurus is unknown. (Part of the predentary of AMNH 5372 (S. parksi) is known but the dorsal border is not preserved (Brown and Schlaikjer 1937).) Also, although a single, distorted predentary is known from Pachyrhinosaurus, Langston (1975) neither describes nor figures this element in sufficient detail to allow a comparison with Centrosaurus. (Unfortunately, the lower jaws of Arrhinoceratops also are unknown, so it is not possible to say if this genus had an intermediate position with respect to this character, as it does with respect to the rostral.)

Both the rostral and predentary elements in ceratopsids show deep and extensive vascular markings that most authors (e.g., Hatcher, Marsh and Lull 1907; Ostrom 1966) have interpreted as an indication of the presence of a horny sheath in life. Ostrom (1966, p.291) felt that "the lack of sharp edges along the beak margins in fossil ceratopsians suggests that the horny beaks may not have been sharp-edged cutting structures" but in fact, the ridges on ceratopsian beaks are just as sharp as those of sea turtles, which do function as cutting edges (Ostrom 1966) so it is possible that each ridge supported a sharp horny rim in life. (Such edges could have been serrated, as in some chelonians, although there is no structural evidence indicating the presence of serrations in the ceratopsian beak.) Whatever the form of the edges of the ceratopsid beak, it would seem that two basic designs existed: that seen in Centrosaurus, and possibly in Styracosaurus, and that found in other ceratopsids. Ostrom (1966, p.292) felt that the ceratopsid beak was adapted for "a grasping or plucking action rather than a biting function" but if the edges of the predentary and rostral did support sharp edges, it would seem likely that these were used for cutting.

The opposing edges of the rostral and the predentary curve in opposite directions, although the degree of curvature is variable. There is a deep depression antero-ventrally in the rostral of all ceratopsids that received the sharp anterior tip of the predentary upon occlusion and the intervening gap between the more posterior edges of the predentary and rostral presumably was filled by the horny sheaths. In Centrosaurus, the ventral premaxillary flange fits, upon occlusion, into the depression between the two dorsal ridges on the predentary whereas in other genera, the long ventral edge of the premaxillary fits into this groove. The ventral premaxillary projection of Centrosaurus lacks the heavy vascular markings found in the rostral and predentary but since it opposes parts of the jaw that presumably were covered with a keratinous sheath, and since the surface of the ventral premaxillary flange is somewhat roughened, it is possible that this projection was at least partially sheathed in keratin as well. The ventral edges of the premaxillaries of other genera probably also were partially sheathed in keratin. Most specimens show at least a slight ridge on this edge, which could have supported a keratinous sheath, and some specimens, such as ROM 5135 (Arrhinoceratops brachyops) (Fig. 32b), show a very distinct ridge, often with striations, ending in a distinct groove that may indicate the posterior margin of the keratinized portion.

In all ceratopsids, it appears that anteriorly, the jaws combined a cutting action with at least some of the grasping function suggested by Ostrom (1966). In all genera, unless the rostral and predentary were covered by keratin in such a way that they no longer possessed sharp edges, the anterior part of the beak had a largely cutting function.

The edges of the bones are sharp and curve in opposite directions. Food caught in between the rostral and predentary would be held firmly, by the opposing curvature of the beak margins, and sheared by the passing of the rostral margin lateral to that of the predentary. In Centrosaurus and Styracosaurus, and possibly in Arrhinoceratops as well, the ventral premaxillary flange probably also was a shearing structure, especially if it was covered in life by a sharp-edged keratinous sheath. The medial surface of the flange would shear past the medial predentary ridge and provide a continuation of the curved anterior cutting edge. All other ceratopsid genera have a fairly blunt ventral premaxillary edge, developed as a long shallow curve. Although it is possible that a keratinous sheath could have produced a sharp cutting edge in this area, from the broad and shallow cross section of the predentary trough, it seems more likely that this was a grasping structure. The more ventral placement of the lateral predentary ridge in Centrosaurus indicates that it acted as a stop for the premaxillary flange but some grasping may have been possible in this area, although not to the extent seen in other genera, where almost the entire ventral edge of the premaxillary would have fitted into the predentary trough.

One of the characteristics of the skull of Centrosaurus, and of Styracosaurus, is the relative shortness of the skull anterior to the jaw articulation.

This fact, combined with the moderately large rostral and the strong ventral flange on the premaxillary indicate that application of force at the beak was more important in these forms than in long-faced species such as *Chasmosaurus belli* and *Anchiceratops longirostris*. In the latter species, the resistance arm (in this case, more or less the entire length of the lower jaw) is very long with respect to the moment arm of the jaw adductors, so that the force that could be generated at the anterior end of the jaws would be less than in a form with a shorter jaw, and hence a shorter resistance arm, such as *Centrosaurus*. Unfortunately, the short-faced species *Chasmosaurus brevirostris* and *Eoceratops canadensis* lack the rostral (the element shown in Lull 1933, pl. VIIA for *C. brevirostris* is a reconstruction) but if this analysis is correct, one would expect a relatively larger rostral in these forms than in *Chasmosaurus belli* or *C. kaiseni*. It is interesting to note that *Triceratops* has a relatively shorter face than *Chasmosaurus belli*, *Anchiceratops* or *Pentaceratops* and the rostral is correspondingly larger, possibly correlated with the fact that a relatively shorter jaw can generate more force at its anterior end.

In many modern herbivorous mammals that can apply force both in the cheek dentition and at the anterior end of the jaws, the lower jaws move anteriorly or posteriorly so that force is applied in only one of these regions at a time (Hildebrand 1974). In ceratopsids, where such motions would be impossible on a large scale, at least at or near full occlusion, at full occlusion force would have to be applied simultaneously over the whole length of the jaws.

Protoceratopsids also are characterized by relatively short jaws and a large rostral, which approaches the form of the rostral of Centrosaurus quite closely, being more or less triangular, with a fairly straight posterior border and a strongly decurved anterior tip. Some older individuals of Protoceratops show a strong ventral flange at the premaxillary-maxillary suture and a similar structure is present in Leptoceratops and Bagaceratops as well. In Protoceratops, the premaxillary teeth lie on this flange and if the function of this flange was similar to that postulated for Centrosaurus, it is possible that these small, peg-like teeth may have had a grasping function.

In ceratopsids, in both the maxillary and the dentary, the anterior teeth are much smaller than those in the rest of the tooth row (see Fig. 28). The most anterior teeth, indeed, are so small that they could not occlude with each other, even upon full adduction of the lower jaws. It seems likely that these very small teeth also functioned in grasping and retaining food, rather than in mastication, although the initial grasping of food would be accomplished by the beak and these small teeth probably merely assisted the tongue in repositioning the food prior to mastication by the larger, more posterior teeth.

On the predentary of Protoceratops, which curves more strongly antero-dorsally than does the predentary of ceratopsids, there are two dorsal ridges, again, with the lateral one more ventrally placed, as in *Centrosaurus*. These ridges are less pronounced and the lateral ridge is relatively less ventrally placed in *Leptoceratops*, which has a smaller premaxillary flange than *Protoceratops*. In *Bagaceratops*, where the predentary is quite small, the ridges are translated back onto the dentary, the ventral ridge merging with the ridge supporting the *M. levator anguli oris*, and the premaxillary-maxillary flange is mostly on the maxillary, above the anterior part of the ventral dentary ridge. The jaws of protoceratopsids are relatively much shorter than those of ceratopsids and the force that could be generated at the anterior part of the beak would be relatively much greater.

The predentary and rostral elements of *Psittacosaurus* are relatively much smaller than those of either ceratopsids or protoceratopsids although their shape is very similar to that of the latter. (These elements are not known from *Protiguanodon*.) There is no ventral premaxillary or maxillary flange in *Psittacosaurus*, however, and the action of the beak seems to have been more simple, maybe one largely of cutting rather than of cutting and prehension.

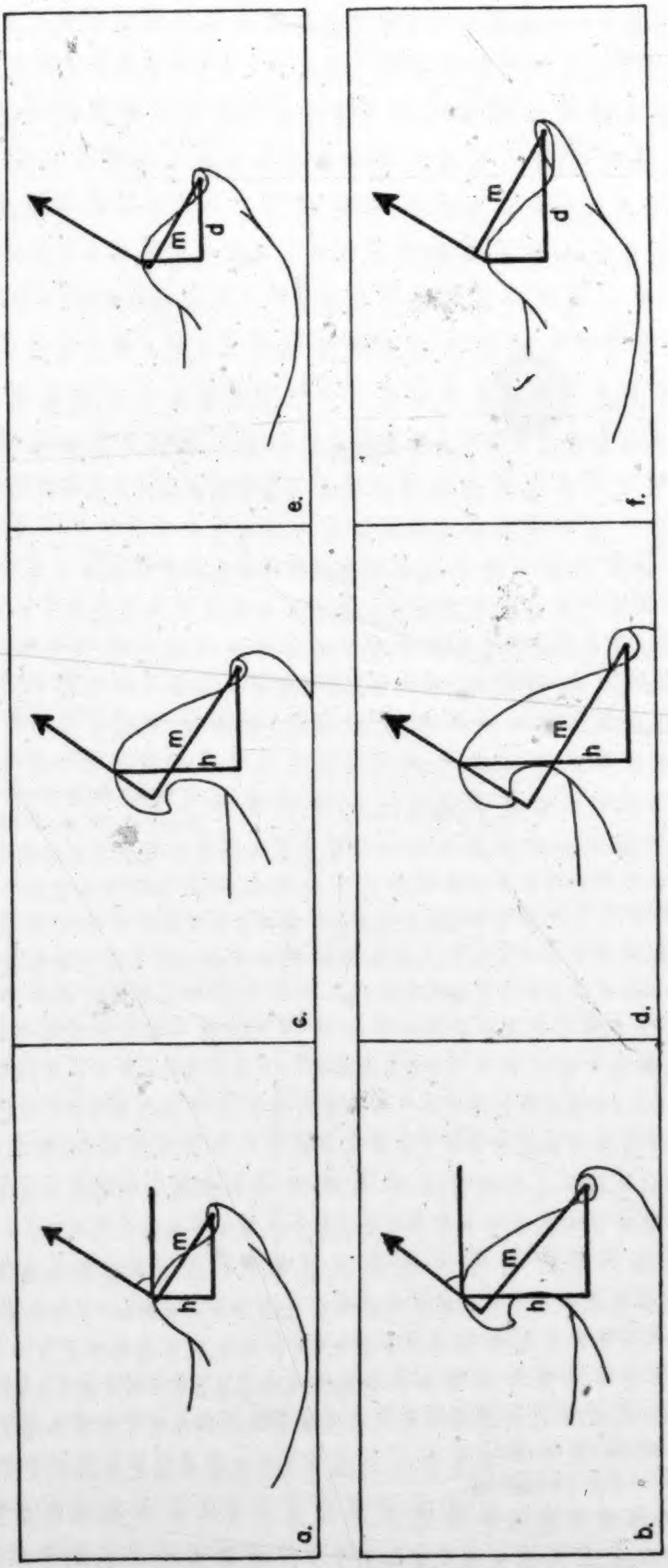
According to Galton (1973), the original function of the predentary probably was to brace the mandibular rami, a function that it retained in all ceratopsians, as shown by its complicated articulation with the dentaries; its function as an element for cutting and prehension presumably evolved later and the very small predentaries of Psittacosaurus and Bagaceratops support this interpretation, since they seem to be less specialized for food gathering than are the predentaries of Protoceratops and the ceratopsids.

Vertebrate jaws act as third class levers, which, as Ostrom (1966) has pointed out, are mechanically less efficient than second class levers because the resistance arm is always longer than the moment arm. Gingerich (1971, p.3) has argued that the vertebrate jaw should be regarded as a link, rather than a lever, because "the relatively long length of the bite lever arm and the great amount of force wasted as reaction force at the jaw joint make this proposed mechanical [lever] system generally very inefficient." Most of Gingerich's argument rests on the fact that the fulcrum, the jaw joint, must be fixed with respect to the skull in order for the lower jaw to act as a lever while in many vertebrates, there is a great deal of anterior-posterior motion possible at this joint. Ceratopsians, however, have neither streptostylic jaws nor large anterior-posterior translatory motions at the jaw joint. The ceratopsian quadrate is strongly fused to the rest of the skull and the predentary-rostral configuration and the fixed, sloping quadrate-glenoid and coronoid process-surangular configuration, effectively prevent anterior-posterior sliding (Ostrom 1966). From the oblique striations on the isolated ceratopsid tooth (APM P64.5.199) and on the teeth of Leptoceratops described above, it appears that a small amount of anterior-posterior motion, in the form of oblique jaw movements, must have been possible in ceratopsians, but on a much smaller scale than in certain modern herbivorous mammals. Thus, the analogy of a lever is applied here to the ceratopsian jaw, although in forms where large-scale anterior-posterior motion at the jaw joint is possible, analogy to a functional link may be more applicable.

In ceratopsids, whereas the tooth row anterior to the coronoid process, and hence to the insertion of the major jaw adductor (M. adductor mandibulae externus), acts as a third class lever, there is a considerable part of the tooth row posterior to the coronoid process, which acts as a second class lever (Ostrom 1964a, 1966). The applied force in such a system is greater than that possible in a third class lever system, implying a very strong moment of force in the posterior region of ceratopsid jaws. The moment of force along the entire tooth row has been increased by increasing the height of the coronoid process, increasing the horizontal distance between the coronoid process and the jaw articulation and depressing the jaw joint below the tooth row (Ostrom 1966; DeMar and Barghusen 1972).

Although the force applied by ceratopsian jaw muscles cannot be determined, one can estimate the relative force by considering the moment arm of the major jaw adductors. "Disregarding friction, the efficiency with which this force transmission is accomplished is determined by the moment arm or leverage through which the adducting or applied forces act upon the lower jaw" (Ostrom 1966, p.302). In all ceratopsids, the coronoid process is very high and received fibres from all three muscles of the M. adductor mandibulae externus. Increasing the height of the coronoid process increases the moment arm (Fig. 33a, b) and depressing the jaw articulation with respect to the tooth row, which increases the functional height of the coronoid process (Ostrom 1966), increases the moment arm still further (Fig. 33c, d). If the area of origin remains the same, increasing the height of the coronoid process will result in an increasingly posterior direction of pull by the adductor muscles (Fig. 33a, b) (DeMar and Barghusen 1972). DeMar and Barghusen felt that the initial pressure selecting for the development of a coronoid process might be concerned more with changing the direction of muscle action than with increasing the moment arm. When the coronoid process is low, in its initial stages of development, pressure selecting for a change in the direction of muscle action may well be more important because the changes in the moment arm produced by increasing the height of a low process are very small (DeMar and Barghusen 1972). In all ceratopsians, however, the coronoid process is well developed and changes in the height of the process would produce larger changes in the moment arm (DeMar and Barghusen 1972). (The coronoid process must be at least "half as high as the distance from the base of

Fig. 33. The moment arm (m) of the major ceratopsian jaw adductors (*M. adductor mandibulae externus*, represented by arrow) can be increased by increasing the height of the coronoid process (h) (a. and b.); by depressing the jaw articulation, which increases (h) (c. and d.); and by increasing the distance (d) from the jaw articulation to the base of the coronoid process (e. and f.).


a.
m
h
b.
m
h
c.
m
h
d.
m
h
e.
m
d
f.
m
d

the coronoid process to the articulation" before the change in the moment arm becomes significant (DeMar and Barghusen 1972, p.624). The height of the coronoid process in all ceratopsians is greater than this minimum value, so one would expect that selection for increasing the moment arm would be a strong factor in the development of a high coronoid process in ceratopsids.)

Depression of the jaw joint in ceratopsids has increased the moment arm further, with respect to protoceratopsids and psittacosaurids, where the jaw joint is depressed only slightly, or not at all, below the level of the dentary tooth row.

Since all interpretations of ceratopsian jaw mechanics have inferred an herbivorous diet and since modern herbivorous mammals also tend not to have the jaw joint on the same level as the tooth rows, at first glance, it would seem likely that these two groups employ similar jaw mechanisms. Modern herbivorous mammals, however, rely strongly on lateral jaw movements, the initial occlusion being essentially simultaneous, followed by a lateral shearing action (Greaves 1974). Also, although ceratopsids have a depressed jaw joint, position of the jaw joint is not the only factor involved in simultaneous occlusion (Greaves 1974).

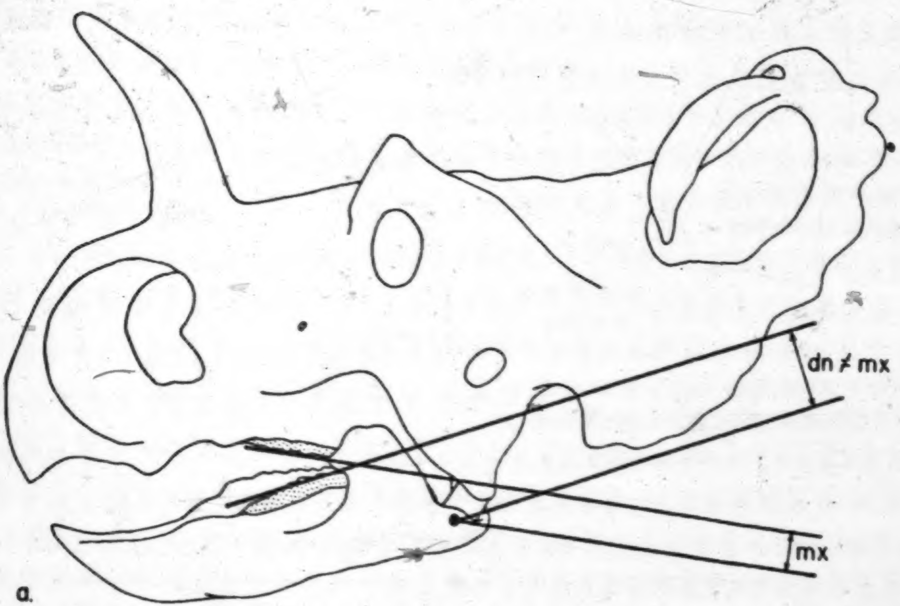
> "If the distances between the tooth rows (or shearing edges of single teeth) and the CMJ [craniomandibular joint] are equal, regardless of whether the CMJ is above ..., below, or on the same level ... as the teeth, the teeth (or

> shearing edges) will meet simultaneously all along the row (or edge). If the distances are not equal ..., or if one tooth row (or shearing edge of a carnassial tooth) is above and the other below ... the CMJ (whether the distances are equal or not) scissor-like shearing will take place"

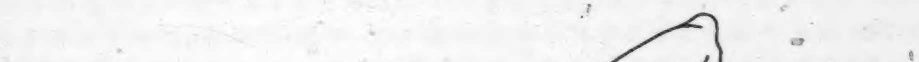
(Greaves 1974, pp.373-4). In no ceratopsian are the distances between the tooth rows and the jaw joint equal (Fig. 34a, b) so that despite the depression of the jaw joint below the dentary tooth row, simultaneous occlusion does not take place. In many herbivorous mammals, the jaw joint is displaced with respect to the lower tooth row and simultaneous occlusion does take place, so Greaves (1974) assumed that although displacement of the jaw joint does increase the moment arm of the adductor muscles, its prime function is to ensure simultaneous occlusion. In ceratopsians, on the other hand, increase of the moment arm of the jaw adductors seems to have been the main selection pressure involved in this development, since simultaneous occlusion does not take place.

The moment arm also can be increased by increasing the distance from the jaw articulation to the base of the coronoid process (Fig. 33e, f) (DeMar and Barghusen 1972). While ceratopsids show a certain relative increase in this distance with respect to protoceratopsids and psittacosaurids, there is a limit to the increase in mechanical advantage that can be achieved by this method, imposed by restrictions of space in the upper jaw and the neccessity of maintaining a certain, minimum gape.

Fig. 34. Left lateral view of skull of a. Centrosaurus and b. Leptoceratops showing that the distance from the dentary tooth row to the jaw articulation (dn) is not equal to the distance from the maxillary tooth row to the jaw articulation (mx). Not to scale. (Tooth rows - stipple; jaw articulation - solid dot.)



a.



b.

Ostrom (1964_a_, 1966), L. S. Russell (1935) and other authors have stated that increase in frill length in ceratopsians, especially in ceratopsids, was related to an increase in length, and hence in power, of the major adductor muscles. While the initial impetus behind the development of a posterior extension of the parietal and squamosal undoubtedly was related to the increase of the major jaw adductors, in later forms, these muscles did not extend posterior to the supratemporal fossae, so that the pressures involved in producing those parts of the frill posterior to the supratemporal fossae must have been related to functions other than mastication (see below).

Another factor influencing the size of the moment arm is the angle at which force is applied to the lever, in this case, the lower jaw.[1] Ostrom (1966) stated that the angle between the direction of pull of the _M. adductor mandibulae externus_ and the long axis of the mandible varied from 30° to 60° in ceratopsians (not including psittacosaurs) and he believed that the posterior extension of the frill in ceratopsids had a significant effect upon this angle. According to the present interpretation, however, only the posterior extension of the supratemporal fossae could be involved in changing this angle. Therefore, no matter what the posterior extent of the _M. adductor mandibulae externus_, the slope of the adductor fossa must indicate the direction of action of the principal jaw adductor, since the muscle must pass through this fossa to reach its point of insertion. In all cases in which authors have reconstructed musculature on the posterior parts of ceratopsid frills, such a reconstruction demands a change in the direction of action of the adductor muscle from that in the fossa to that on the dorsal surface of the frill. Thus, when estimating the principal direction of muscle action, only the slope of the adductor fossa should be considered and changes in the length of the frill cannot be used to explain changes in the angle of force application. An analysis of uncrushed skulls with complete adductor passages and with at least complete posterior regions of the lower jaws would be necessary in order to define trends in the principal direction of action of the major jaw adductors and to attempt to explain their significance. At present, too few specimens meet these criteria to make a complete survey of this feature possible among ceratopsians.

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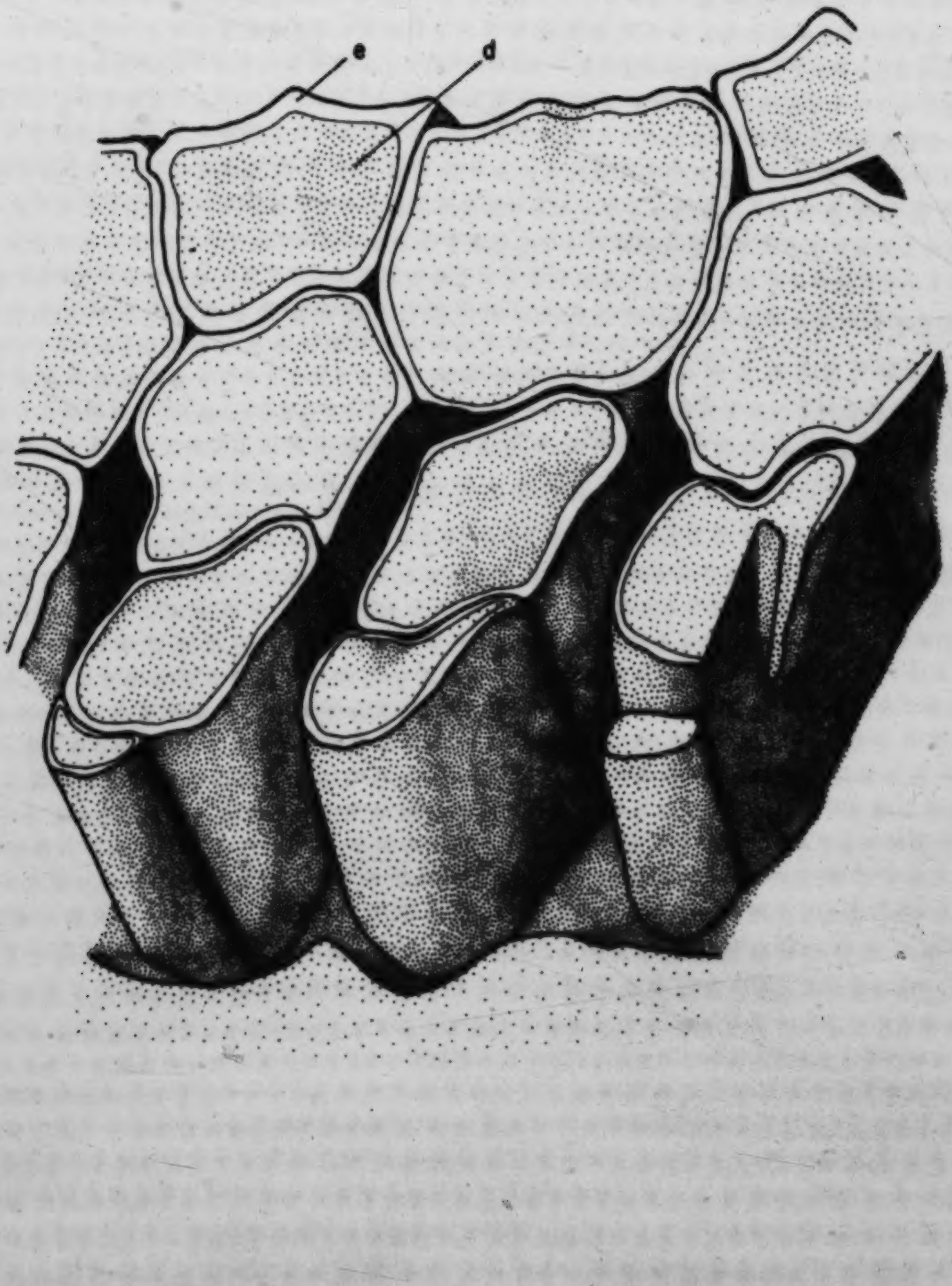
[1] This discussion concerns only the fully adducted jaws. The size of the moment arm and the angle at which force is applied to the lower jaw from the _M. adductor mandibulae externus_ would change during adduction (Ostrom 1966).

In ceratopsids, the ventral margin of the dentary is essentially straight but in psittacosaurids, and especially in protoceratopsids, it tends to be curved. In young individuals of Protoceratops this margin is almost straight but it becomes progressively more convex with age (Brown and Schlaikjer 1940c) until, in old individuals, it becomes highly curved. (The angular is involved in this curvature as well (Brown and Schlaiker 1940c).) Brown and Schlaikjer felt that this change was related to the increasing steepness of the frill with age, which was mentioned above, and the resultant change in the direction of pull of the adductor muscles. Since the adductor muscles of Protoceratops arose from the base of the frill (Kurzanov 1972), however, changing the angle of the frill with respect to the rest of the skull would have little, if any, effect on the direction of pull of these muscles, and certainly not enough effect to produce such a distinctive feature as the strongly curved dentary. Also, the dentary of hadrosaurs is strongly curved, as well (although it is decurved) and hadrosaurs have no great posterior extension of the M. adductor mandibulae externus origin, so some other factor must be involved in producing a highly curved ventral dentary margin, although the functional interpretation of this feature is obscure.

Despite the fact that the major component of jaw action in ceratopsids was vertical, there are sufficient departures from purely vertical wear surfaces in the teeth to indicate that some variations occurred in this action. As mentioned above, large-scale anterior-posterior motion was not possible in ceratopsid jaws, although Lull (1908) felt that some lateral motion was possible in the initial stages of adduction. The glenoid surface in ceratopsid mandibles is transversely oriented (Ostrom 1964a) and probably allowed a small amount of lateral motion. At occlusion, the largely vertical wear surfaces would prevent such lateral motion but prior to complete adduction, a certain amount of lateral movement would be possible and presumably such motion was the cause of the variations in wear surfaces. In *Leptoceratops*, and possibly in other protoceratopsids, variations in tooth wear indicate that a considerable amount of such lateral movement was possible, at least in certain individuals, producing a variety of wear facets other than those generally described as characterizing the genus. Nonetheless, even in *Leptoceratops*, the orientation of the wear surfaces is fairly even, at least in the anterior and medial portions of the tooth row (McKenna and Love 1970), indicating the existence of some mechanism to prevent large-scale lateral movements. As mentioned above, there is sufficient room in the ceratopsian skull to permit the development of a large *M. pseudotemporalis*, rather than the "ribbon" of muscle postulated by Haas (1955), and the *M. pterygo-mandibularis* seems to have been well developed in all genera. It would seem likely that the main action of these muscles, especially of the *M. pterygo-mandibularis*, which would have had a large anterior component of force, was restraint of the jaws, preventing extreme lateral motions caused by unequal contraction of the adductor mandibulae externus muscles.

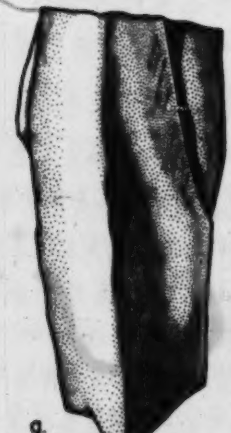
The form of the ceratopsid dentition implies a jaw action in life that was a unique blend of the vertical shearing motions seen in modern carnivorous mammals with certain features characteristic of modern mammalian herbivores, such as a strongly developed mandibular adductor, relatively weaker "pterygoideus" muscles and a jaw articulation that is not in line with the tooth rows. Such a combination is not found in any extant vertebrate, comparable features being developed only in the extinct hadrosaurs. Both hadrosaurs and ceratopsids have a tightly interlocked tooth row, although a very large dental battery is developed in hadrosaurs, and both have edentulous portions of the jaws, the anterior ends of which were capped with horny sheaths in life. In each, one surface of the tooth is marked by a strong median ridge, with smaller anterior and posterior ridges, and there is a very strongly developed coronoid process. While there are similarities between the jaws and dentitions of these two groups, however, there are important differences as well, which imply both different food gathering and masticating actions and a different diet. The essentially straight shearing edge, oblique occlusal plane and larger number of teeth involved in the occlusal surface of hadrosaurs have been mentioned already but the wear surfaces on the individual teeth also vary from those seen in ceratopsids. Although both Lull and Wright (1942) and Ostrom (1961) have stated that the teeth of hadrosaurs bear enamel only on the ridged surface, in fact, there is a layer of enamel surrounding the crown, although the layer on the ridged surface is much thicker. In consequence, when hadrosaur teeth become worn, the enamel forms a slight ridge that surrounds a gently hollowed basin, formed by dentine (Fig. 35). Ostrom (1961)

Fig. 35. Oblique occlusal view of dentary teeth of unidentified hadrosaur (UA 11734) showing extent of enamel (e) and dentine (d) on worn occlusal surfaces. (Labial surfaces in foreground.)

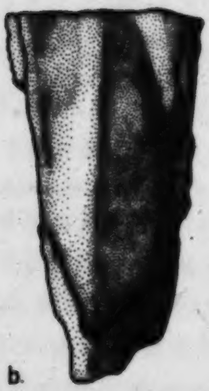

e
d

has presented convincing evidence that the main jaw action in hadrosaurs was one of anterior-posterior grinding. If Ostrom's interpretation is correct, the shallow basins formed by the worn crowns would capture small particles of food, which would be rolled and crushed by the action of the jaws, the rotation of the particles in turn deepening the wear surfaces in the dentine. In ceratopsids, the major jaw action was one of vertical shear, chopping food rather than grinding it. The presence of enamel on one tooth surface alone produces a planar occlusal surface, edged with enamel, an adaptation for slicing rather than grinding actions. These very different jaw actions in hadrosaurs and ceratopsids are reflected again in the manner of tooth replacement. Hadrosaurs have a broad, inclined occlusal surface, suitable for grinding, and the arrangement of the teeth in the vertical tooth series is such that several teeth in the same series can be used at once. Thus, there is none of the rotation of the occlusal surface of individual teeth seen in ceratopsids, but rather, the orientation of the wear facets in hadrosaur teeth is more or less the same, no matter what the age of the tooth (Fig. 36). Although the jaw articulation is depressed below the dentary tooth row in both groups, it is interesting to note that the distances of the tooth rows from the jaw articulation are much more nearly equal in hadrosaurs than in ceratopsians (Fig. 37), so that occluson would be almost, although not quite, simultaneous (see above). Since the major jaw action in

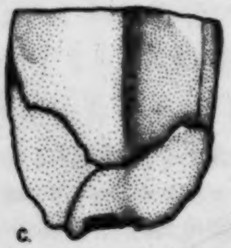
Fig. 36. Functional series of isolated teeth (UA 207) illustrating the lack of rotation of the occlusal plane in hadrosaurs. (Compare with Fig. 26.) a. and d., x2.56; b. and e., x2.56; c. and f., x2.75.



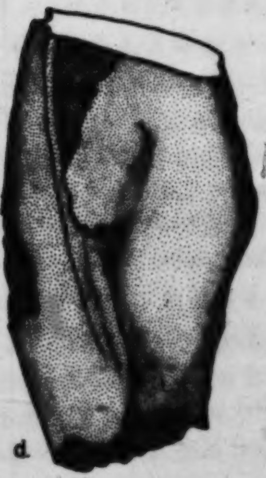
a.



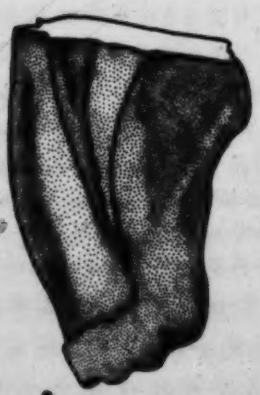
b.



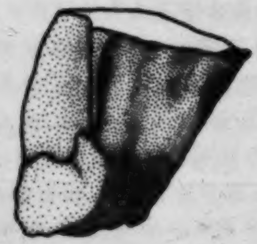
c.



d.

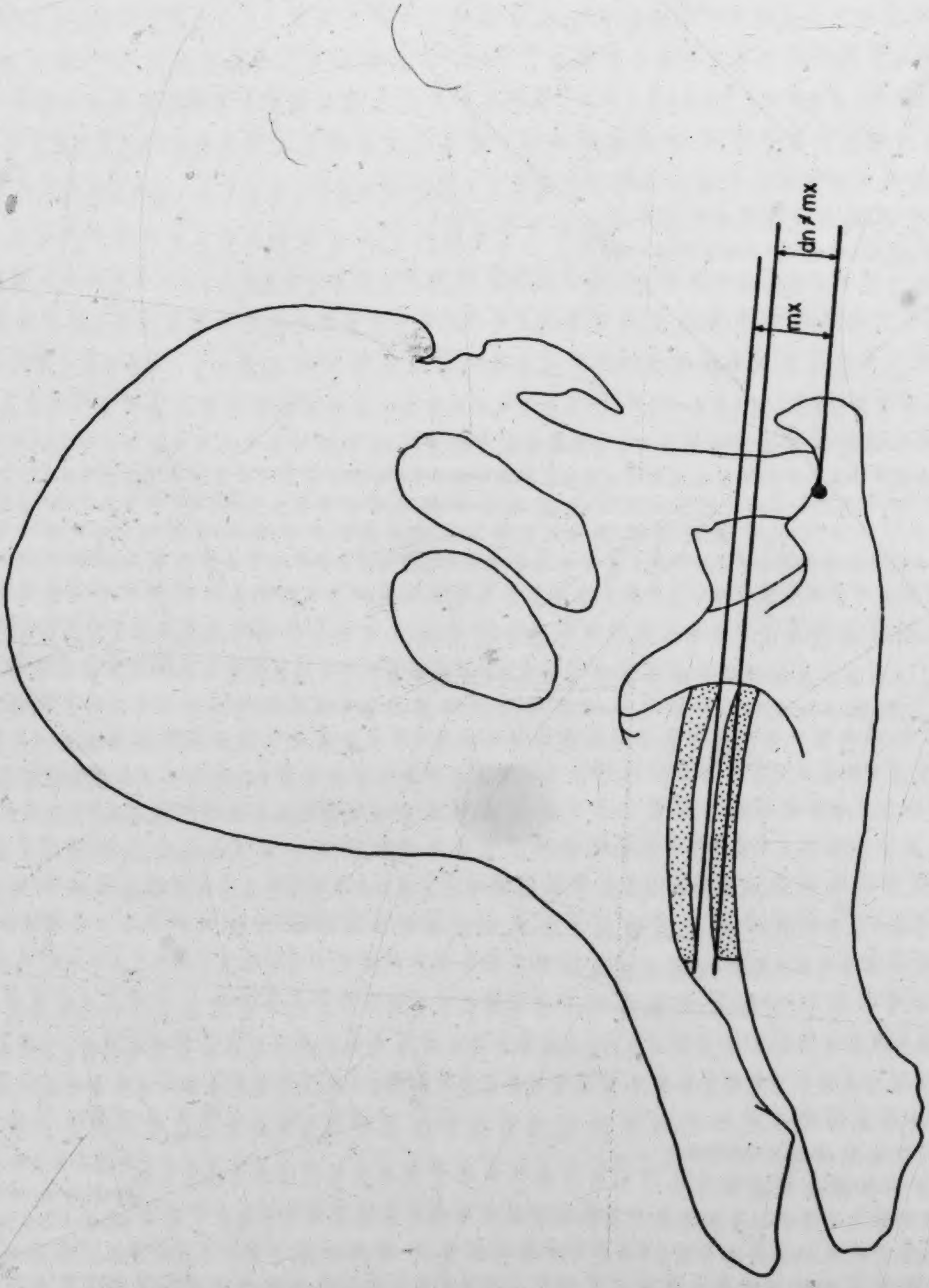


e.



f.

Fig. 37. Left lateral view of skull of AMNH 5240 (*Corythosaurus casuarius*) (from Ostrom 1961) showing that the distance from the dentary tooth row to the jaw articulation (dn) is close to but not equal to the distance from the maxillary tooth row to the jaw articulation (mx). (Tooth rows - stipple; jaw articulation - solid dot.)


mx
dn ≠ mx

hadrosaurs was one of grinding after initial tooth-on-tooth contact, one would expect a system of simultaneous, or almost simultaneous occlusion, whereas in ceratopsians, one would expect a shearing occlusion.

Such differences in the jaws and dentition also imply differences in diet between hadrosaurs and ceratopsians. There is some debate over the diet of hadrosaurs. The first and still the most persistent hypothesis (see, for example, Colbert 1951) proposes soft aquatic vegetation as the principal food of hadrosaurs. While there is no reason to believe that hadrosaurs could not utilize such food items, Ostrom (1961, 1964b) felt that the extensive dental batteries indicate a diet consisting largely of resistant materials that would wear away individual teeth rapidly, rather than soft tissues that would require little mastication. Colbert (1951) suggested that hadrosaurs might have fed on shelled molluscs as well as aquatic plants but Ostrom (1964b) felt that resistant, perhaps even woody plant material formed the main portion of the hadrosaur diet. Certainly, hadrosaurs may have utilized a wide variety of food items but the presence of such an extremly specialized dentition seems to indicate that they had a strong preference for a particular kind of food and, as Ostrom (1964b) has pointed out, among modern mammals, dentitions that form extensive grinding surfaces are correlated with a diet of siliceous, fibrous and/or woody plant tissues, so one may infer a similar diet for hadrosaurs.

Ostrom (1966) postulated a similar diet for ceratopsids but it is possible that there was a higher fibre content in the preferred foods of ceratopsids since while "crushing and grinding are effective means of reducing most edible plant tissues to small, easily digested particles, ... highly fibrous tissues are best cut or sliced" (Ostrom 1966, p.306). While one can compare many features of the hadrosaur dentition to the dentitions of certain modern mammals, the ceratopsid dentition has no close modern analogs and despite certain similarites between the dentitions of hadrosaurs and ceratopsids, dental function was very different in these two groups. The type of vertical shear producing the most characteristic wear facets seen in ceratopsid teeth occurs today only in largely carnivorous mammals but other features of ceratopsid cranial anatomy strongly suggest that ceratopsids lacked adaptations for capturing live prey. According to the present interpretation, ceratopsids possessed lateral cheeks that covered almost the entire tooth row. While such a cheek undoubtedly had a certain amount of elasticity, its very bulk would restrict the gape, and modern vertebrates that capture live prey invariably possess a wide gape (and lack extensive lateral cheeks). Further, the arrangement of masticatory muscles postulated for ceratopsids indicates an herbivorous rather than carnivorous diet. Several authors have commented on the correlation between highly developed "temporal" muscles and herbivorous habits and highly developed "pterygoid" muscles and carnivorous habits and while the Mm. pseudotemporalis and pterygo-mandibularis of ceratopsids were well developed, the muscles of the adductor mandibulae externus group were much larger and more powerful muscles. Although ceratopsids appear to have had the simple vertical jaw movements characteristic of the "kinetic inertial" type of jaw action seen in carnivores (Olson 1961), they probably had many more of the characteristics of the "static pressure" system seen in herbivores: highly developed "posterior adductors" (adductor mandibulae group); no "anterior pterygoid" muscles; a strong coronoid process; and well developed "middle adductors" (Mm. pterygo-mandibularis and pseudotemporalis). In such a system, the greatest force is exerted when the jaws are at or near a fully occluded position (Olson 1961). Thus, shearing in ceratopsids would not be a matter of rapid slicing movements but of powerful shearing at occlusion. This combination of vertical shear plus a static pressure system is not found among modern mammals and reptiles.

(d) Stress transmission in ceratopsian skulls

Having looked at the mandibular mechanics of the ceratopsian skull, it is necessary to investigate the stresses set up by mastication (and other functions) in order to understand the structural responses of the skull to functional requirements. Tucker (1954, 1955, 1956), Frost

(1964, 1971, 1973) and others have shown that the responses triggered by a stress-causing function may be far-reaching, affecting areas quite distant from the initial source of stress. Bearing this fact in mind, it is necessary to look at ceratopsian skulls in more detail before analyzing patterns of stress and the responses they invoked.

In discussing the structure and function of a skull, one must consider the sutures between bones, as well as the bones themselves. "Varieties of sutural area patterns correspond in some fashion to the nature of the forces which are normally imposed upon them and to the response to these forces which they allow" (Moss 1957, p.570), so that degree of sutural closing, sequence of sutural closing and configuration of sutural areas may give an indication of the functional demands made upon different areas of the skull.

Open sutures, which still have soft tissue between the adjacent bones, allow changes of size and shape to take place in the skeleton during growth. In birds and most mammals, sutures generally close by ossification when growth ceases but some (cr most, as in the case of marsupials) may remain open throughout the life of the individual (Hildebrand 1974). In ceratopsids, it appears that some sutures remained open throughout an individual's lifetime, while other sutures invariably are fused in any adult skull. Many authors have attempted to use degree of closure of sutures as an indication of age in ceratopsians and indeed, for almost all ceratopsians, this is the only criterion that is even partially reliable. In genera other than Protoceratops, there are too few specimens for size, increasing number of teeth, change in proportions and similar features to be good criteria for age determinations and nor is degree of vascularization of the skull useful in this respect (see above), so if one is to determine the relative age of an individual ceratopsian (other than Protoceratops), the determination must be based upon the condition of the sutures. Therefore, if a general sequence of closure of cranial sutures could be established, it would prove useful in estimating the relative ages of individual specimens.

Direct examination of specimens, combined with a search of the literature, showed that although there may be variations in the timing of the closure of specific sutures in ceratopsids, one can formulate a general sequence of sutural closure. (I made no such attempt for protoceratopsids or psittacosaurids.) In ceratopsids, the dorsal sutures between corresponding elements on either side of the skull fuse at a relatively early age. The parietals are coalesced in all individuals and never show any indication of a mid-line suture. If the single, median parietal element of ceratopsids was formed from more than one center of ossification, it gives no indication of such an origin in any known skull. (In very young specimens of Protoceratops, the anterior extremity of a mid-parietal suture may be visible (Brown and Schlaikjer 1940c), so presumably, the parietal of ceratopsids also represents the fusion of paired parietals, but no mid-line suture is visible in any ceratopsid.) Elements anterior to the parietal tend to fuse along the dorsal mid-line as well. Even in YPM 1821 (*Triceratops flabellatus*), a young individual with almost all the cranial elements disarticulated, the postorbitals and frontals are fused together dorsally, both along the mid-line and along the sutures between the postfrontals and frontals, as well. The very anterior portion of the dorsal suture between the frontals is visible in YPM 1821 (see Hatcher, Marsh and Lull 1907, pl. XLV), indicating that such fusion proceeded in a posterior to anterior direction, as did fusion of the parietals in *Protoceratops* (see above), and probably in ceratopsids generally. In AMNH 5401 (*Chasmosaurus kaiseni*), apparently an older individual than YPM 1821, judging by the number of sutures that are closed or partially closed, the dorsal suture between the two frontals is fused and the suture between the two nasals (including the nasal horn core) is completely obliterated, as well. (Analysis of the sequence of sutural closure in the area between the brow horn cores is complicated by the presence of the frontal fossa and secondary roofing over the braincase. When these features are considered (see below), it becomes apparent that absolute size and certain other features also are important in determing the rate and sequence of coössification in this area. Although these features may be related to age, they distort any sequence of closure based on age alone.)

This coössification of the dorsal skull roof probably was correlated with the function of the horn cores. Coössification of the skull roof, first between the brow horn cores, then progessing anteriorly to include the area between the brow and nasal horn cores, would provide an increasingly strong platform to support the often massive horns, which must have increased in size and weight with age. A firmly coossified platform supporting the horn cores may have functioned in three ways: to provide support for the brow horns; to provide a sturdy brace to resist forces and to disperse evenly stresses caused by impact when the horns were in use (either as weapons or in other active functions); and to prevent flexure between bones (Giblin and Alley 1944), either from the weight of the horns or from forces generated during their use. According to Currey (1962b), sharp discontinuities in a structural element raise local stresses considerably, and if the discontinuity is a notch, as in the case of the cross section of a partially fused suture, this effect is even more pronounced. For this reason, generally "those parts of bones ... that are most likely to suffer from high stresses, are smooth" (Currey 1962b, p.115). Thus the presence of sutures in a structure functioning to resist large stresses should be relatively uncommon and if one considers the skull roof between the three horn cores as a functional unit, it is reasonable to expect that the sutures in this area of the skull would be among the first to close.

Although parts of the ceratopsid parietal may be extremely thin, the central area, presumably the original sutural area, is always thickened, forming a mid-dorsal ridge that gives structural support to the rest of the frill. Early fusion of the parietals, if more than one center of ossification was involved, probably was related to the need to provide a strong framework for the frill from a very early stage in ontogeny. Despite the fusion of the parietals, however, the squamosal-parietal suture remains open until relatively late in the life of an individual and the exoccipital-squamosal and at least part of the exoccipital-parietal suture may remain open for a considerable time, as well. While structural support for the frill would be essential at all ages, demanding a certain degree of rigidity in the frill, study of the many specimens of *Protoceratops* (Kurzanov 1972; Brown and Schlaikjer 1940*c*) has shown that there can be extensive ontogenetic variation in ceratopsian frills, affecting size, shape and orientation with respect to the rest of the skull. The frill sutures, other than any that may have existed within the parietal, probably remained open to allow such changes to take place.

Some parts of the ceratopsid occiput also fused quite early in life. Langston (1967) stated that the lack of sutures in the occipital condyle of a specimen of *Pachyrhinosaurus cf. P. canadensis* housed in the Drumheller and District Museum in Drumheller proved that this specimen was an adult but in fact, sutures within the occipital condyle are known only in YPM 1831 (*Torosaurus* "*gladius*" (=*latus*, see Colbert and Bump 1947)) (see Hatcher, Marsh and Lull 1907, fig. 7). Indeed, the presence of visible sutures in the occipital condyle at a more or less adult stage (YPM 1831 has a very large skull) may be an individual aberration of this specimen. Even in YPM 1821 (*Triceratops flabellatus*), the occipital condyle shows no sutures and the sutures between the exoccipital and basioccipital are obliterated in the areas adjacent to the condyle as well.

Again, one can explain this early fusion in terms of the stresses affecting this area. Although the *ligamentum nuchae*, *M. spinalis capitis* and other muscles attaching to the occiput would support much of the weight of the head, a large part of this considerable weight would have been borne by the occipital condyle and large stresses would develop in this structure and in adjacent parts of the occiput. In the condyle itself, the presence of sutures would concentrate more and more stress in a restricted area as the weight of the skull increased, so the occurrence of such sutures in a skull as large as that of YPM 1831 (*Torosaurus* "*gladius*" (=*latus*)) is surprising. Although the suture between the parietal and the exoccipital and in some cases, even between the exoccipital and supraoccipital can be open, the fusion of the two exoccipitals, basioccipital and occipital condyle would provide a strong support for the weight of the head.

Some of the stresses created by this weight could have been distributed to other parts of the skull (see below) but since the largest forces would occur in the immediate vicinity of the condyle, this is the first area of the occiput where coössification would occur.

The posttemporal fenestra, which in many reptiles carries a vein from the area of the occiput to the lateral wall of the braincase (Romer 1956), is closed in ceratopsids, probably in correlation with the need for strength in the occiput. Also, in all ceratopsids, the three most anterior cervical vertebrae are coalesced (Lull 1933) (see Fig. 23), a condition that probably developed to help the anterior part of the vertebral column bear the enormous weight of the head.

The other area of the ceratopsid skull that is always at least partially coössified is the braincase. Coössification in this area can be explained with reference to the two sources of stress mentioned above: the weight of the head, causing large stresses in the occipital region, and the weight and use of the nasal and brow horn cores, causing stresses in the dorsal skull roof. The braincase is immediately adjacent to both these areas and since the contents of the braincase are so delicate, structural support and reduction of stress in this area would be extremely important. The sutures between the exoccipitals and the laterosphenoids, the laterosphenoids and the basisphenoids, and the two laterosphenoids are coössified, as far as is known, in all ceratopsids (Hatcher, Marsh and Lull 1907) and the opisthotic and prootic are so thoroughly coössified with the rest of the braincase that Hatcher (Hatcher, Marsh and Lull 1907) did not even mention these elements in his discussion of the ceratopsid braincase. Hatcher (Hatcher, Marsh and Lull 1907) thought that parasphenoid elements were present in ceratopsids, fused into the laterosphenoids ("alisphenoids") and Hay (1909) felt that presphenoids and orbitosphenoids were present in the anterior regions of the braincase. These elements may well be present, representing centers of ossification that originally were separate from other parts of the braincase, but if so, they also are thoroughly fused into the braincase in all known ceratopsids.

One other suture in the ceratopsid skull seems to have fused at a very early age and that is the suture between the vomers. The vomers are long slender elements lying along the mid-line of the palate and generally they are not preserved in ceratopsid skulls but they are known in at least three specimens. In 1903, when Lull described the skull of AMNH 970 (Triceratops serratus), he stated that only a single vomer, with a deep median keel, was present. Hatcher (Hatcher, Marsh and Lull 1907, p.29) disagreed with this interpretation since the "vomer" of YPM 1820 (T. horridus) "shows on its inferior side a distinct median suture" and probably, the element described by Lull (1903) represents paired vomers, fused throughout their length, with the ventral keel corresponding to the area of fusion. YPM 2016 (Chasmosaurus belli) also possesses fused vomers (Lull 1933) and early fusion between these elements probably characterized all ceratopsids.

The suture between the vomers and the pterygoids is visible in YPM 1820 (Triceratops horridus) (Hatcher, Marsh and Lull 1907) and the suture between the fused vomers and the maxillaries of AMNH 970 (T. serratus) is visible (Lull 1903), so probably the vomers of ceratopsids did not fuse to other elements as early in ontogeny as they did to each other. From the very delicate nature of the vomers, it seems unlikely that they were important stress-transmitting elements in the ceratopsid skull. More likely, the thin strut formed by the vomers helped support soft tissues while the major stresses affecting the palate were transmitted through the more robust premaxillaries, maxillaries, palatines and pterygoids.

On the lateral surface of the skull, the more dorsal sutures, especially near the anterior orbital rim, tend to close before the more ventral sutures but there is considerable variation in the precise sequence of closure.

The lower jaw shows a fairly distinct pattern of its own. The predentary-dentary sutures fuse relatively early; the articular, prearticular and surangular tend to fuse together (Brown and Schlaikjer 1940a) and "the intercoronid tends to fuse with the dentary and coronoid, but the splenials, angulars, and coronids unite with other elements along squamous sutures with smooth surfaces that readily separate from each other" (Brown and Schlaikjer 1940a, p.2). The fact that the major sutures between the dentary and the more posterior bones of the lower jaw remain open for a long time in the life of an individual probably accounts for the fact that the post-dentary bones often are missing, even when the rest of the lower jaw is well preserved.

Despite individual variations, then, it is possible to define a general pattern of sutural closure that is correlated with the relative age of an individual ceratopsid specimen. Specimens in which the central occipital sutures, the braincase sutures, the suture between the vomers or the dorsal mid-line sutures are open are relatively very young individuals, although the pattern of closure along the dorsal mid-line is modified by the frontal fossa and closure in this region was affected by factors other than age (see below). On the other hand, specimens with all the post-dentary sutures (including sutures with the dentary) fused and/or the more ventral sutures of the facial and postorbital regions fused are relatively old individuals.

As mentioned, the pattern of sutural closure along the dorsal mid-line is disrupted by the secondary roofing over the braincase. In all ceratopsids, except Brachyceratops, there is a space between the original dorsal surface of the skull and the surface separating the brow horn cores. (In Brachyceratops, as in the protoceratopsids, there is a depression on the dorsal skull roof that is a precursor of the secondary roofing of other genera.) As with the braincase, it is difficult to interpret the composition of this area, not only because it is so highly modified with respect to the dorsal skull roof of other reptiles but because the bones involved in the secondary roofing generally are thoroughly fused to each other (Sternberg 1927a). This coössification is especially noticeable in Triceratops (Sternberg 1927a), which formed the basis of much of the early work on this region of the skull. Since this area has been interpreted in several different ways, the terminology is quite variable. Here, following Sternberg (1927a), the space between the braincase and the secondary roofing is termed the frontal fossa and any opening in the secondary roofing that communicates with the fossa is termed the frontal fontanelle.

Although all ceratopsids possess either a frontal fossa or a clear precursor to it, not all specimens have a frontal fontanelle. In YPM 1822 (Triceratops prorsus), for instance, the frontal fontanelle is closed and the frontal fossa is completely sealed off from the dorsal surface of the skull (Brown and Schlaikjer 1940c). In NMC 8795 (Centrosaurus longirostris, on the other hand, the frontal fontanelle is only partially closed, with a short posterior section remaining open (Sternberg 1940). The condition in this specimen indicates that closure of the frontal fontanelle was a gradual process in all ceratopsids, probably beginning anteriorly. Such closure could well be correllated with age and indeed, both Lull (1903) and Erickson (1966) felt that closure of the frontal fontanelle in YPM 1822 (*Triceratops prorsus*) indicated that this specimen, although small, was fully adult. By 1933, however, Lull had decided that closure of the frontal fontanelle could not be correlated with age because in YPM 1821 (*T. flabellatus*), certainly a very young individual, the frontal fontanelle is closed. Probably, the factor involved is not absolute age but the weight of the brow horn cores and the stresses involved in their use. Sternberg (1929, p.37) noted that in ceratopsids "where the brow horns are large the frontal fontanelle is usually nearly or completely closed." In all ceratopsids possessing brow horn cores, the size and weight of the horns very probably increased with age so that closure of the frontal fontanelle sometimes may have coincided with the onset of maturity. In some species, however, such as *Triceratops flabellatus*, the brow horn cores were extremely long even in juveniles so that closure of the fontanelle would occur at a much earlier age.

In YPM 1830 (*Torosaurus latus*) there are two small, posteriorly-facing fontanelles, although in YPM 1831 (*Torosaurus* "*gladius*" (=*latus*)) there is only one. Possibly this variation is due to a more advanced stage of closure in YPM 1830, in which an originally single fontanelle has been divided by anterior growth of the parietal. Certainly the anterior part of the parietal projects farther forward in this specimen than in YPM 1831 (compare Hatcher, Marsh and

Lull 1907, figs. 118 and 119) and Hatcher (Hatcher, Marsh and Lull 1907) regarded YPM 1830 as the older individual. Since the frontal fontanelle of different specimens is in different stages of closure, there is considerable variation in the size and shape of the fontanelle within the Ceratopsidae but probably the original shape of the fontanelle varied somewhat as well since in YPM 1834 (Triceratops brevicornus) the "fontanelle is large and circular in outline" (Hatcher 1905, p.415) while in Styracosaurus it is long and rectangular (see Lull 1933, pl. VIIIB). Since the fontanelle is at least partially closed in almost all specimens, it is inadvisable to use variation in this feature as a taxonomic character although in some cases, such as Styracosaurus (Lambe 1913), the fontanelle has quite distinctive characteristics. Further, this area often is distorted by lateral crushing, as in UA 40 (Eoceratops), so that any taxonomically significant features would be damaged or destroyed.

The frontal fossa itself varies among ceratopsids, even within one genus, in its connections with the supratemporal fossae. The skull of AMNH 5116 (Triceratops elatus), part of a composite skeleton mounted at the American Museum of Natural History, has a large frontal fontanelle connected to the supratemporal fossae by deep passages but AMNH 970 (T. serratus) has only slight indications of connecting passages with the supratemporal fossae and in YPM 1822 (T. prorsus) there is no trace of such connecting passages (Brown and

Schlaikjer 1940c). Probably, in all young ceratopsids (except Brachyceratops) the frontal fossa was connected to the supratemporal fossae but, like the frontal fontanelle, these connections gradually coössified with age. The rate of this closure was much more variable than the rate of closure of the frontal fontanelle and seems to have been largely independent of the fontanelle, since there are specimens, such as YPM 1830 (Torosaurus latus), with deep connecting passages but very small frontal fontanelles.

In most ceratopsids, the frontal fossa is completely separate from the brain cavity so that the designations "pineal foramen" (Hatcher, Marsh and Lull 1907)[1] and "pseudopineal fontanelle" (Lull 1933) are wholly inappropriate and although there is often a connection with the supratemporal fossae, Hay's (1909) application of the term "supratemporal fossa" to the frontal fossa also is incorrect, for there is no ventral opening in the frontal fossa for the transmission of the adductor muscles (Sternberg 1927a). In at least one specimen, however, there is a large foramen connecting the frontal fossa and the braincase. Gilmore (1919, fig. 1) illustrated, in longitudinal section, the braincase and frontal fossa of USNM 5740 (an unidentified species of Triceratops), showing a large, well-preserved foramen in this position. As far as is known, this condition is unique among certatopsians and possibly, it is an individual abberation peculiar to this specimen although the edge of the foramen is smooth so that the condition does not seem to have had a pathological cause. (Sternberg also examined this specimen and confirmed Gilmore's (1919) description (Sternberg 1927a).) At present, there is no adequate explanation for the presence of this foramen in this specimen.

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[1] Lull himself (Hatcher, Marsh and Lull 1907) noted that a term such as "postfrontal fontanelle" would be more appropriate although Marsh generally used the terms "pineal" or "parietal foramen".

Endocranial casts[1] show distinct, elongate processes that "appear to be vertical extensions of the cerebellum" (Brown and Schlaikjer 1940c, p.193) although those of Protoceratops are much smaller than those of Anchiceratops and in neither specimen do they appear to represent extensions of the brain but rather sinuses separate from the frontal fossa (Brown and Schlaikjer 1940c). Endocranial casts of ceratopsians are rare, so it is not possible to determine the distribution of this feature within the Ceratopsia but Hay (1909) showed that there are similar processes in Triceratops, although Hay interpreted these as part of the cerebellum.

The other connection with the frontal fossa involves the brow horn cores. In AMNH 5251 (Anchiceratops ornatus) the frontal fossa "opens into a large central chamber on each side underneath the supraorbital horns. These passages are entirely enclosed and do not communicate with the supratemporal fenestrae, but in front they communicate with the orbital cavity", although these cavities do not penetrate the braincase (Brown 1914a, p.541). The frontal fossa of AMNH 970 (Triceratops serratus) also is continuous with hollows in the brow horn cores (Lull 1903) but according to Sternberg (1940, p.472): "in most Belly River ceratopsians the horncore is not hollow, and the frontal fossa is completely separatated from the base of the horn by the folded frontal".

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[1] In all reptiles, endocranial casts are not a true reflection of the size and shape of the brain and so can only be used to give a very general description of the brain's anatomy (Jerison 1969).

The fossa itself may not vary greatly among ceratopsids (other than Brachyceratops) in its basic form, although generally, this area is not visible, since the skull must be sectioned or broken away to expose the fossa in its entirety. Lull (1903, pp.691-692) provided the following description of the frontal fossa of AMNH 970 (Triceratops serratus):

> "It [the fossa] is more or less wedge-shaped, tapering dorso-ventrally as one goes forward, the anterior limit being just in front of the orbit. The flat roof is formed by the overlying postfrontal [postorbital] and frontal bones, while the sinus is laterally constricted into three chambers. The anterior chamber has a rather flat floor and is separated from the median chamber by vertical pillar-like bones, one on either side, which serve also to support the antero-internal portions of the horn-cores. The floor of the second or largest chamber is deeply excavated, and it is this chamber which communicates with the horn-core sinuses by openings in the lateral walls. The posterior chamber, lying just beneath the fontanelle, is small and round, and in the specimen in question has a small pencil-like bone running obliquely from the left lateral wall to the floor, after the manner of a flying buttress."

It is not possible to describe the frontal fossa in most ceratopsids in such detail but where portions of the fossa can be seen, they agree closely with the above description, varying mostly in their connections with other spaces in the skull. NMC 1254 (*Eoceratops canadensis*), as mentioned above, shows the right wall of the frontal fossa, which is divided into three chambers, as in AMNH 970 (*Triceratops serratus*), although there is no connection with the brow horn cores, which probably are solid as in UA 40 (*Eoceratops canadensis*). The floor of the fossa is not preserved in NMC 1254 (*E. canadensis*), but the anterior chamber is smaller, indicating that the fossa may have tapered anteriorly, as in *Triceratops serratus*. As in *T. serratus*, the middle chamber is the largest and the divisions between the chambers also are similar to those of *T. serratus*. In USNM 5740, the specimen of *Triceratops* illustrated by Gilmore (1919), the wall of the fossa is similar to those described above but the middle chamber is relatively larger, owing to the connection with the brain cavity. Probably, the basic pattern of the frontal fossa was similar in all ceratopsids.

There has been much debate concerning the composition of the frontal fossa, partly due to the extent of coössification in this region and partly due to confusion over the placement of the parietals and the identity of the bone forming the median part of the frill. The interpretation accepted here is that given by Sternberg (1927*a*), based on *Styracosaurus*. There are variations in shape and proportions of individual bones but the basic pattern appears similar throughout the Ceratopsidae (except for *Brachyceratops*). Therefore, Sternberg's (1927*a*) description of *Styracosaurus* is given as a general description, since in NMC 344 (*S. albertensis*) "all of the bones of the floor and sides [of the frontal fossa] are splendidly preserved and the sutures well shown" (1927*a*, p.139). The frontal fontanelle in *Styracosaurus* lies within the frontals, not the postorbitals ("postfrontals"), the frontals having folded dorsally to form the secondary roofing (Sternberg 1927*a*). Posteriorly, part of the floor of the frontal fossa is formed by the coalesced parietals and "at their anterior extremity the parietals meet the frontals at the base of a cross buttress of the frontals, which has been formed to support the secondary roof, with a transverse suture which extends across the width of the floor of the fontanelle and then runs diagonally back, out and up to meet the antero-internal angle of the parieto-postorbital union .... This suture between the frontals and parietals, which in *Protoceratops* is approximately at right angles to the midline of the skull, has been deflected backward by the posterior development of the postorbitals and frontals" (Sternberg 1927*a*, p.140).

While certain features of the secondary roofing are fairly constant throughout the Ceratopsidae, however, the development of this region in *Brachyceratops* is unusual. The first described specimens of *Brachyceratops* (Gilmore 1914,

1917) were juveniles, so that the unusual development of the frontal fossa in these specimens could be interpreted as ontogenetic variation. Since these initial descriptions, Gilmore (1939) has described USNM 14765, an adult specimen of *Brachyceratops montanensis*, but unfortunately, he did not describe or figure the dorsal skull roof and did not mention the presence of a dorsal depression, so the condition of the skull roof in adult *Brachyceratops* is still uncertain. In those specimens of *Brachyceratops* where the dorsal skull roof has been described, then, there is no secondary roofing but there is a depression, sharply set off from the rest of the skull roof by a conspicuous ridge (Gilmore 1914, 1917). In the type specimen of *B. montanensis* (USNM 7951), Gilmore (1917) described a fontanelle in the posterior part of the dorsal depression but it seems likely that this fontanelle is actually a post-mortem break, as no smooth edge is preserved (see Gilmore 1917, fig. 6).

The character of the dorsal depression of *Brachyceratops* is much closer to the condition seen in protoceratopsids than to that seen in other members of the Ceratopsidae. Some specimens of *Protoceratops* show a slight depression on the dorsal surface of the skull, where the frontals and parietals unite, with the depression approximately equally divided between the two elements and bounded anteriorly by a low ridge (Brown and Schlaikjer 1940*c*). This depression deepens with age, becoming more rounded anteriorly and more extensively developed so that it includes almost one third of the dorsal surface of the frontals (Brown and Schlaikjer 1940c). Not all *Protoceratops* skulls show a dorsal depression, however, although this area usually is at least somewhat smooth and concave and Brown and Schlaikjer (1940c) concluded that the presence of a dorsal depression was a sexually dimorphic character, with the skulls lacking a strongly developed depression belonging to the "females". According to Kurzanov (1972), in the *Protoceratops* skulls in the collections of the USSR Academy of Sciences Paleontological Institute, there is considerable variation, probably individual variation, in this depression and there is a skull in this collection (Specimen 614-6) with "female" characteristics (no incipient nasal horn core, a narrow frill, a dorso-ventrally narrow face) that possesses a deep fronto-parietal depression. Therefore, although this depression varies with age and between individuals, if it varies between sexes it probably varies only with respect to the absolute size of the individual, being relatively deeper in larger individuals. Gilmore (1939) described a similar but even deeper depression in *Leptoceratops* but only one specimen of *Bagaceratops* shows a frontal depression and again, this is a large specimen (Maryanska and Osmolska 1975).

Most authors (*e.g.*, Sternberg 1927a; Brown and Schlaikjer 1940c; Kurzanov 1972) agree that this dorsal depression of the skull roof in protoceratopsids is the precursor of the frontal fossa and secondary roofing of the

Ceratopsidae. Although from the composition and position of the depression between the orbits, this interpretation seems likely, the very different configuration of these two features indicates at least a partially different function.

Several functions have been proposed for the frontal fossa of ceratopsids. Brown (1914b) suggested that blood vessels supplying the horn cores passed through this area but as Sternberg (1940) has pointed out, in many genera there is no connection between the frontal fossa and the horn cores, since the horn cores are not hollow. In those genera where the horn cores are hollow and do connect with the frontal fossa, it is possible that blood vessels were transmitted in this manner but since, with the exception of *Brachyceratops*, the frontal fossa is fairly similar throughout the Ceratopsidae, it is likely that its primary function also was similar throughout the family. Sternberg (1940, p.472) remarked that Dr. T. H. Eaton, Jr. (presumably, in a personal communication) "suggested that the frontal fossa may have been the place of origin of an anterior division of the adductor muscle." Sternberg (1940, p.472) appeared to support this interpretation, or at least find it acceptable, stating: "it is worth noting that this excavation runs from the supratemporal fenestra to the frontal fossa", implying that since the supratemporal fenestra was filled with muscle, the same may have been true for the frontal fossa. While it is highly probable that the entire supratemporal fossa of ceratopsids was filled with jaw adductor muscles, it is difficult to see what advantage to the adduction of the lower jaws there could be in bringing a slip of these muscles forward to attach to any portion of the frontal fossa. Such a muscle would be small and weak, and would lie in such a postion that it would add little, if anything, to the effectiveness of the main muscle mass. If muscles did attach in this area, therefore, and there is evidence for such an interpretation in some species, such muscles would not have been involved in jaw adduction. In *Centrosaurus* and *Styracosaurus*, the anterior edge of the median parietal bar has two smooth depressions. (These depressions are relatively small in *Centrosaurus* but they are much larger in *Styracosaurus*.) The form and texture of these depressions strongly suggests that they served for muscle attachments, although the possible function of such muscles is obscure and certainly was not connected with adduction of the lower jaws.

Several authors (*e.g.*, Brown and Schlaikjer 1940*c*; Langston 1975) have suggested that the secondary roofing served to protect the braincase and to strengthen the region between the brow horn cores. Although the secondary roofing of ceratopsids is an unusual feature, it is not unique since some modern artiodactyls show comparable features. Whatever other functions were performed by ceratopsid horns, from the similarity in external form of the horns of many ceratopsid genera and certain modern bovids, it appears likely that ceratopsid horns could have been used as offensive weapons.

Even if this interpretation is incorrect, indisputably the brow horn cores must have added considerable weight to the dorsal skull roof, producing additional stresses on the skull. In modern horned bovids, especially those that engage their horns and head in active combat, there is "a pneumated skull with a double roof of bone over the brain" (Geist 1966, p.559). This space serves to protect the brain from the stresses produced by active use of the horns and the division of this space into chambers allows the stress to be divided and transmitted by the individual bony struts. Certainly, not all ceratopsids have large brow horn cores that would place heavy weights on the skull and it is impossible to be sure what functions these smaller horns performed but the similarity in form and the correlation between the presence of horns and the "pneumatized" skull roof between those horns and the braincase in two such different groups as ceratopsids and bovids strongly suggests that there was a similar function - stress transmission - and possibly, a similar cause, as well - agressive contact with head and horns - even in short-horned species. In Brachyceratops and the protoceratopsids, however, it seems unlikely that a shallow depression could have functioned in this manner. Further, these genera never show large brow horn cores, although there is no evidence to indicate that they did not engage in head-to-head combat. Possibly, the frontal depression developed in response to entirely different selection pressures than those that produced the frontal fossa and certainly the very different form suggests a different function. Perhaps this depression supported a pad of soft tissues but at the moment, there is no evidence to indicate the function of this structure.

Before analysing the major stress patterns in ceratopsian skulls, there is one more feature that must be examined. In determining how an open suture will function under stress, it is important to determine the form of the sutural area involved. There are several different classifications for sutural form but the classification used here is from Hildebrand (1974), who divided sutures into five structural types (although a single suture may be a complex blend of several of these types): a butt joint is formed when two approximately square edges meet, forming a straight suture on the surface of the bone; if one edge overlaps the other, a lap joint is formed but this is an unusual configuration in animals (Hildebrand 1974); usually, if the edges of two elements overlap, each edge tapers to form a scarf joint; a peg-and-socket joint (or gomphosis) is formed by the insertion of one element into a depression in another; and a serrate joint is formed by the interdigitation of two edges. (Moss (1957) considered serrate joints to be merely a special form of butt joint but since the mechanical properties of the two types are rather different and hence they occur under different conditions in the skull, Hildebrand's classification is used here.)

In experiments with rats, Moss (1957) discovered that cranial sutural morphology could be altered by experimentation, from which he concluded that the form of a suture is a response to the forces imposed upon it. Certainly the mechanical properties of the different sutural types vary widely so despite the fact that ceratopsian skulls cannot be subjected to the same type of experimental analysis used by Moss, one can infer what types of stresses dominated particular areas by the form of the sutures involved.

Of the five sutural types outlined above, lap joints are unusual among animals because "when a lap joint is compressed or tensed, the area of contact is not evenly stressed" (Hildebrand 1974, p.450). Therefore, this discussion is confined to the four other sutural types. Butt joints are strong in compression but very weak in shear or bending; scarf joints "often join thin flat bones" (Hildebrand 1974, p.450) and are much stronger (and occur more frequently in skulls) than lap joints, since "the entire area of contact is evenly stressed by most loads" (Hildebrand 1974, p.450); peg-and-socket joints are strong in compression and shear if the elements involved are hard, fairly thick and not flat; and serrate joints form strong unions "between roofing bones of the cranium of some tetrapods, particularly of amphisbaenians (which dig with the head) and artiodactyls (which support horns or antlers)" (Hildebrand 1974, p.451). Again, such a joint would be strongest in compression but the interdigitation of the two edges would add to the overall strength of the joint, as well.

Unfortunately, complete, disarticulated skulls are rare among the Ceratopsia, so one cannot determine the range of variation in form of particular sutural areas and since the visible sutures are variable, most likely the sutural areas were quite variable as well. Nonetheless, several specimens show at least some sutural areas and YPM 1821 (_Triceratops flabellatus_) has a large number of disarticulated cranial elements, so in certain cases it is possible to examine the relationship of sutural form to the stresses imposed upon the skull.

Predictably, lap joints are unknown in the ceratopsid skull but scarf joints are quite common. The nasal-premaxillary sutures appear to be scarf joints in all ceratopsids, as one would expect from the flat, thin nature of the main body of the nasals. The dorsal nasal-premaxillary junction is a simple scarf joint with the premaxillary overlapping the nasal, although the nasal may be slightly grooved for the reception of the premaxillary. There is little variation in this joint in ceratopsids. The ventral nasal-premaxillary union is always more extensive than the dorsal union and often it is quite complex as well. In _Triceratops_ _flabellatus_ the nasal merely overlaps the premaxillary but in _Eoceratops_ _canadensis_, the premaxillary sends up an elongate process that interdigitates with two similar processes on the nasal. The form and relationships of this premaxillary process are highly variable in ceratopsids and Lull (1933) noted that even within a single genus, Centrosaurus, the exact shape of this process is variable.

Other scarf joints in the ceratopsid skull include the union of the maxillary and jugal (the jugal overlapping the maxillary, which may be slightly grooved so that this union becomes almost a tongue-and-groove arrangement); the dorsal union of the nasal and prefrontal (the nasal overlapping the prefrontal, often quite extensively); the union of the jugal and postorbital (the jugal overlapping the postorbital); the jugal-quadratojugal-quadrate area (the jugal overlapping the quadratojugal and the quadratojugal overlapping the quadrate); and many of the sutures in the lateral wall of the braincase, which, where visible, appear to overlap quite extensively (see Hatcher, Marsh and Lull 1907, fig. 24). In fact, scarf joints are easily the most numerous form of sutural union in the disarticulated ceratopsid skulls available for study.

Butt joints also are common and in some areas grade smoothly into scarf joints in which there is little overlap of elements. Butt joints in ceratopsid skulls are most common along the dorsal mid-line: between the nasals; between the premaxillaries; between the epinasals in Eoceratops canadensis; and between the frontals where any of the frontal-frontal contact is preserved. (Since the dorsal sutures between the brow horn cores fuse early in ceratopsids, it is not possible to tell if this area also formed butt joints or if serrate joints were present, as in horned artiodactyls.)

In contrast to scarf and butt joints, serrate and peg-and-socket joints are relatively uncommon in ceratopsid skulls. The posterior part of the ventral union of the two maxillaries may be a serrate joint, as in *Triceratops serratus* (see Hatcher, Marsh and Lull 1907, fig. 26) and many of the sutural areas in the lower jaw are peg-and-socket joints.

The unions between the rostral and premaxillaries and between the predentary and the dentaries are complex. Dorsally, the rostral sends a flange between the premaxillaries, which meet in a butt joint throughout the rest of the length of their dorsal edges but ventrally, the rostral forms a socket for the reception of a "peg" formed by the anterior portions of the premaxillaries. The predentary joins the dentaries in a series of complex scarf joints that in some cases verge upon peg-and-socket joints.

Klaauw (1948, p.1) regarded the skull as "a complex of relatively separate functional components" but while it is possible to analyze the form and function of these components separately (*e.g.*, braincase, teeth and jaws, nasal region, and so on), other authors (*e.g.*, Tucker 1954, 1955, 1956) have analyzed the skull as a single functional unit, emphasizing the way the skull as a whole responds to and is shaped by the stresses caused by the various cranial functions. Both approaches have their merits and in fact, a comprehensive analysis would require a blend of the two. In ceratopsians, however, as in many groups of extinct organisms, the functions of certain areas of the skull are obscure so that a complete analysis is impossible. If one regards the ceratopsian skull as a single unit, though, it is possible to determine, from the gross structure of the skull and without reference to particular functions, the major patterns of stress transmission within the skull.

In brittle materials, such as bone, the concentration of stresses is an important design factor, much more so than in ductile materials, because if ductile materials yield locally to imposed forces, they will flow plastically and the stress will be spread more evenly (Currey 1962b). (Normally, concentration of stresses in ductile materials is important only in causing fatigue fractures (Currey 1962b).) Brittle materials, however, are susceptible both to fatigue fractures and to sudden ruptures caused by loading beyond the strength of the material.

Evans (1957, p.5) defined stress as the "intermolecular resistance within an object to the action of an outside force which is applied to it." Stress cannot be seen or measured directly but its magnitude can be computed by various formulae (Evans 1957). Strain, on the other hand, is a change in shape within an object caused by a force applied to the object (Murray 1936) so the magnitude of strain can be measured directly. Stress and strain each occur in three basic forms: compression, tension and shear. All other stresses and strains may be reduced to combinations of these three types (Frost 1964). Compression stress resists shortening in an object under a compression load; tension stress resists elongation under a tension load; and shear stress resists the motion of one part of an object past another part (Currey 1962b). Strains may be defined in a similar manner. When force is applied to an object, no matter how complex the system of forces applied, there are two directions of principal stress at every point in any planar section of the object. These directions are mutually perpendicular, with the stress in one direction being a maximum tension (minimum compression) stress and that in the other direction being a minimum tension (maximum compression) stress (Murray 1936). A third stress, a shearing stress, will be produced in any directions other than those of the principal stresses (Murray 1936).

While there is a consensus that stress produces a reaction in bone, there has been much debate as to the exact form of such reactions. Washburn (1947) experimented with removing the M. temporalis on one side of the skull of day-old rats. Among his results, Washburn noted the following: where some fibres were not removed, vestigial crests, processes and so on developed; both size and shape of the bones to which the M. temporalis normally attaches and the sutural areas around such bones altered during the course of the experiment; some features associated with muscle attachment failed to develop while others, already present at the beginning of the experiment, were resorbed. From these results, Washburn concluded that bone has the ability to respond, sometimes very extensively, to mechanical stress (or lack of stress) and he classified the anatomical features of bone into three groups according to their stress-induced reactions: those features that are never present unless their associated muscles are present; those that are "self-differentiating", like the coronid process, and are present from birth but require the continued presence of their associated muscles to be retained; and those that are largely independent of mechanical factors, their presence being determined entirely by the original genetic information determining the shape of the bone. (These three classes may grade into each other and different aspects of a single feature, such as length, width and size of processes of attachment, may fall into different categories (Washburn 1947).)

Although he emphasized that bone does respond to mechanical stress, Washburn made no attempt to define different types of stress, or to define a mechanism by which bone responds to stress on a cellular level, nor did he indicate that differing responses might be due to different conditions of stress. Liskova and Hert (1971) reviewed some of the theories on the reaction of bone to stress, noting that, unlike Washburn's work, most of the earlier theories assumed that tension rather than compression stress is most important in stimulating a response in bone, while later papers placed tension in a position of secondary importance and some modern papers have claimed that one cannot distinguish between the effects of tension and compression stress "because both forces ... act upon bone alternatively" (Liskova and Hert 1971, p.302). (This last view is the one espoused by Liskova and Hert, on the basis of experimental results involving loading of the tibiae of young rabbits. Liskova and Hert argued that one cannot distinguish between the effects of compression and tension because compression along one principal axis is always accompanied by tension along the other sc that "pressure and tension, therefore, lead to a similar state of strain in tissue".[1])

Epker and Frost (1965) also discussed the reaction of bone to imposed forces, remarking that there are inconsistencies in the approaches of different authors to this problem. To illustrate this point, Epker and Frost (1965) gave four clinical examples (taken from human anatomy) showing varying responses of bone to compression:

[1] It is important to note that this discussion is concerned with the cellular response of bone, _i.e._, bone deposition or resorption, to stress and not with the fracturing of bone under stress, which definitely is strongly correlated with the type of stress involved for as Currey (1959, p.88) remarked: "from the biological point of view it is nearly always the tension strength of bone that is important." Bone is a brittle material and is much stronger in compression than in tension because "minute Griffith cracks in the material cause intense stress concentrations, and so will spread under the influences of tensile stresses, which tend to open up the cracks, but not under the influence of compressive stresses, which will tend to force the sides of the crack together" (Currey 1962_a_, p.513).

1. A fractured long bone, healed such that there is an unnatural concavity on one surface, will respond to compressive forces on its concave side by depositing bone in the concavity.

2. A tooth socket subjected to pressure on one side (e.g., by orthodontic appliances) responds by resorbing bone on the side of the socket subjected to compression.

3. In walking, the human os calcis (calcaneum) is subjected to large compression forces on its plantar surface but normally, neither bone loss nor bone formation accompanies the imposition of these forces.

4. Mastication causes compression forces in teeth and tooth sockets but the teeth respond by exfoliating with age, rather than by becoming more deeply seated in the jaw due to resorption of tissue in either the tooth or the tooth socket.

Since one can demonstrate so clearly that the response of bone to compression is variable and that there is no consistent correlation between type of stress (or strain) and the bone's response, Epker and Frost (1965) suggested that compression (or tension) itself may not be responsible for the bone's reaction. There is a factor that is consistently correlated with bone reaction, however, and that is change in the surface curvature of the bone (Epker and Frost 1965). "Increased concavity is consistently associated with bone formation. Decreasing concavity is consistently associated with resorption" (Epker and Frost

1965, pp.37-39). Bone is deposited by osteoblasts but the osteoblasts in turn are derived, by changes in the nucleus, from osteoclasts that are formed by the mesenchymal cells distributed throughout bone (Frost 1964). When bone is loaded by the imposition of external forces, two changes occur in the surface of the bone: a deformation in both compression and tension, and a change in the surface curvature (Frost 1964). "The mesenchymal cells are activated by the compression or tension induced change. Selective inhibition of osteoclastic or osteoblastic activity is caused by the bending change, the particular case depending on the direction of the bend" (Frost 1964, pp.16-17). Thus, either compression or tension will induce a response in the mesenchymal cells (although in practice, net compression is more usual than net tension (Frost 1964)), with greater deformation causing increased activation, although "the activation signal seems to be unaffected by the absence or presence of simultaneous bending of the surface" (Frost 1964, p.18). It is unlikely that the change in surface curvature itself causes the response, but the work of Bassett and Becker (1962) indicates a possible cause since these two workers showed that the polarity of electrical potentials generated in stressed bones varies with the direction of bending, so possibly it is an electrical signal that triggers the actual cellular response. (According to Frost (1973, p.320): "when lamellar bone undergoes flexure parallel to its grain the outer surface of the concave tending side develops a negative electrical charge, that of the convex tending surface a positive one".) In the present study, only surface texture and shape of bones was studied and no attempt was made to analyze cancellous bone or the relation of stress to the pattern of trabeculae. (Lack of specimens that can be sacrificed for sectioning makes such a study impractical, at least on a large scale, at the present time.) Therefore, Frost's theories (the "flexure drift law") are used here only in conjunction with the surface topography of lamellar bone.

Frost himself has noted that there are various modifications and restrictions that must be applied to this "law". First of all, "the relationship between the direction of the maximum compression strain[1] and the direction of the longitudinal grain of the bone is important in deciding the effective strength of the activation signal generated by a given strain" (Frost 1964, p.75). Secondly, bone destruction occurs parallel to the longitudinal grain of the bone, and parallel to the direction of compression, with little interference from the surface geometry of previously deposited bone, but bone deposition adapts to the local surface contours, with little interference from the direction of grain or deformation (Frost 1964). Thirdly, according to Frost (1973, p.325): "the flexure drift law applies only to lamellar bone surfaces directly covered by

[1] Note that Frost correlates all behaviour with strain, rather than stress, as do most other authors.

overlying soft tissues" and it does not apply where the surface of a bone is covered by cartilage (i.e., at all joint surfaces; at tendon, ligament and fascia attachments; and on either side of epiphyseal plates and apophyses; in all of which the "chondral growth/force-respose characteristic" obtains); nor where the bone surface is covered by a tooth, although edentulous surfaces respond to the drift law; nor where the bone surface is bare, as in a wound. Finally, this law does not govern change in the overall length of a bone (Frost 1973).

Another important factor in determining the reaction of bone to stress is the duration of the stress. Liskova and Hert (1971) showed that continuous stress applied experimentally to the tibiae of rabbits did not produce a reaction in the bone, even after a year, supporting the theory "that only dynamic, i.e., intermittent action, constitutes a morphogenetic stimulus to bone apposition" (Liskova and Hert 1971, p.314).

While Frost's flexure drift law can be applied to clinical situations, in which bending in an abnormal direction or to an abnormal degree produces a pathological condition in bone, it also can be used to analyse the "normal" shape of a bone, bearing in mind the fact that other influences, such as the limiting effect of neighbouring tissues (Murray 1936), will affect the shape of a particular bone as well.

Some of the stresses developed in the ceratopsian skull were relatively very large, judging by the thickness of associated areas of the skull, the complexity of some sutural areas and the early fusion of other sutures. Probably, the following stresses were among the most important in the ceratopsian skull: stresses caused by the function of the major jaw adductors, including stresses caused by the resistance of food items during mastication as well as stresses caused by the pull of muscle on bone; stresses caused by the weight and active use of the horn cores; and stresses caused by supporting the massive head and frill, including the stresses generated by the muscles supporting the head and stresses produced in the occipital condyle.

Contraction of the major jaw adductors would produce stresses at all areas of attachment (primary stresses), at the quadrate-articular joint (secondary stresses), and in the jaws, where resistance of food would produce opposing forces that would set up tertiary stresses (Tucker 1954). These stresses may be subdivided further into circumscribed and dispersed stresses (Tucker 1954). Circumscribed stresses are large but limited to a relatively small area, so that "they are resisted not only by the structures they act directly upon. They are transmitted sometimes to the distant points of the skull. Accordingly, various structures develop for the transmission of these stresses" (Tucker 1954, p.387). Dispersed stresses, on the other hand, may be large as well but their immediate action affects a relatively large area and so they "are resisted at the very place, or close to the place, of their origin" (Tucker 1954). Thus, the stresses that develop in the areas of origin of the *M. adductor mandibulae externus* are primary dispersed stresses for although the size of the adductor passage indicates that this muscle complex was very large and could generate large forces, the area of origin is large and probably little, if any, of the stress generated in this region was transmitted to other areas of the skull.

In all ceratopsids, there is a greatly thickened area at the angle between the dorsal and lateral (squamosal) walls of the supratemporal fossa. While it is not possible to determine the exact limits of the areas of origin of all the divisions of the *M. adductor mandibulae externus* (see above), the lateral and dorsal walls of the supratemporal fossa undoubtedly participated in the origin of the more lateral fibres of this complex, the smooth inner surfaces of these walls indicating a broad, fleshy origin, producing stresses that were evenly distributed, rather than concentrated in certain areas, as is the case with tendinous attachments. Since parts of the *M. adductor mandibulae externus* attached to both dorsal and lateral walls of the supratemporal fossa, contraction of the *M. adductor mandibulae externus* would bend the angular area in between so that its medial surface became increasingly concave, resulting in bone deposition on this medial surface. In addition, however, the lateral surface of this angular area often is thickened as well and this lateral thickening cannot be accounted for by the action of the *M. adductor mandibulae externus*. In fact, according to the flexure drift law, one would expect bone destruction in this area, so this "extra" thickening must have a cause other than contraction of the major jaw adductors. In all ceratopsids, the thickened, angular portion of the squamosal, as well as forming part of the wall of the supratemporal fossa, lies directly in line with the brow horn core, the anterior part of the thickening merging smoothly with the base of the horn core. The exact uses of these horn cores will never be known but if, by analogy to modern horned artiodactyls, ceratopsids used their horns aggressively, to drive off predators or to combat other ceratopsids, the stresses produced would be circumscribed as the brow horn cores are small with respect to the rest of the skull, and so these stresses would have to be transmitted to other parts of the skull. According to Tucker (1955), mammalian skulls transmit stresses *via* arches, ridges and other bony thickenings and the thickness of the angular area of the squamosal of ceratopsid skulls probably had this function, as well. Certainly, some ceratopsids have small or negligible horn cores but even in these forms it is possible that the brow horn core area was used in an essentially similar way, producing similar stresses that would have to be transmitted to other areas of the skull, away from the delicate tissues of the brain. (Not all stresses would be transmitted by this thickened area, though, as the well developed frontal fossa undoubtedly participated in this function, as well.)

Unlike the area of origin of the _M_. _adductor_ _mandibulae_ _externus_, the area of insertion of the major jaw adductors of ceratopsids is relatively small, with a powerful Bodenaponeurosis concentrating most of the fibres, and the stresses, on the dorsal part of the coronoid process. At first glance, the presence of a large process at the area of attachment of a muscle is puzzling. According to the flexure drift law, contraction of a muscle should make the surface of attachment more convex and hence initiate bone destruction, forming a concavity, not a process. As mentioned above, however, the flexure drift law does not apply to areas of bone covered by tendon. Between a tendon (or ligament, fascia or aponeurosis) and the supporting bone surface there is a layer of calcified cartilage, closest to the bone, and a layer of hyaline cartilage, closest to the tendon, which Frost (1964, p.36) termed a "mesenchymal cell barrier", since these two layers exclude mesenchymal cells from the supporting bone surface. When the muscle contracts, therefore, although the supporting surface becomes more convex, there are no mesenchymal cells to be activated by the stresses so produced, so the relative thickness of the bone does not change, but the adjacent surfaces that are not covered by tendon become increasingly convex as well and these surfaces are subjected to bone destruction, so that a process develops beneath the tendon (Frost 1964). The coronoid process of ceratopsids is not just a passive structure, however, for it is thick as well as tall and probably served to transmit the large stresses produced by the jaw adductors into the robust body of the dentary, as well as increasing the mechanical advantage of the jaw adductors.

Although a large component of the force applied to the coronid process is vertical, there is a considerable posterior component, as well. In connection with this component it is interesting to note that the posterior edge of the coronoid process is braced by a large surangular, the long axis of which lies at a 45° angle to the long axis of the coronoid process (see Fig. 16), almost at right angles to the average direction of pull of the _M_. _adductor mandibulae externus_ complex, so that the surangular resisted the tendency to postero-ventral rotation of the coronoid process.

In his analysis of mammalian skulls, Tucker (1955) defined three types of skulls: breviarcuate, longoarcuate and planoarcuate, on the basis of the way the skull transmits the stresses developed in mastication. (Actually, "the real difference between the functional skull types is in the _intensity_ of stresses per unit area of bone resistance" (Tucker 1955, p.531).) According to Tucker (1954, pp.383-4): "the resistance of food ... against the force which originates from masticatory muscles creates stresses which radiate into the surrounding bone ....

Consequently stresses appear in defined areas of the mandible and maxilla. Those areas betrayed, in ... decalcified skulls, the existence of stresses by detectable structural transformations. Hence the defining of postion, by the stresses and morphological character depending on this, is possible and justified." Tucker (1954, 1955, 1956) was concerned mainly with mammalian skulls but he did mention that the hadrosaur Edmontosaurus showed certain of the characteristics of the planoarcuate skull. Ceratopsians also show planoarcuate characteristics (lack of distinct cranial arches (other than the zygomatic or jugal arch), horizontal jugal arch, teeth of approximately equal length and similar shape forming two large occlusal surfaces[1]) and so certain parts of Tucker's analysis apply to ceratopsians as well.

The stresses caused by mastication in modern planoarcuate skulls are large but local "and do not provoke the formation of accessory structures", although these stresses do "influence the increase of existing bony masses" (Tucker 1955, p.523). Ceratopsids also conform to this pattern to some extent, the fact that the teeth are similar throughout the tooth row indicating that the masticatory stresses were dispersed, as in modern planoarcuate skulls, and were resisted locally (Tucker 1954). Further, the maxilla and dentary of ceratopsids are beam-like and massive, with thickened alveolar ridges, as in other planoarcuate skulls, an adaptation to resisting large but local and dispersed masticatory stresses. (In the mammalian skulls studied by Tucker (1955), such thickened areas proved to be denser as well but the density of bone in different parts of the ceratopsian skull has not been investigated.) In planoarcuate skulls, the areas not involved in resisting masticatory stresses evolve relatively independently (Tucker 1955) and certainly the roof of the ceratopsid skull and the postorbital portion of the skull seem to have developed independently from the stresses created in the jaws, showing no specialized structures for transmitting stress from that region. The nasal region, on the other hand, does not seem to have been affected by masticatory stresses, as it is in the modern planoarcuate skull (Tucker 1955), for there is no osseous median septum bracing the dorsal nasal region. Also, although the area immediately anterior to the orbit may be thickened, as in _Eoceratops_, it is more likely that this thickening is a response to stresses caused by the nasal and brow horn cores, rather than by stresses transmitted from the maxillary tooth row, since the region between the dorsal, thickened area and the tooth row often is very thin. While most masticatory stresses probably were resisted locally in the ceratopsid skull, however, some may have been transmitted by the maxillary ridge, to be dissipated in the flat jugal and postorbital bones.

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[1] In this respect, hadrosaurs are closer to a true planoarcuate type than are ceratopsids, in which the teeth do not form a continuous occlusal surface and occlusion is neither simultaneous nor nearly simultaneous (see above).

It is interesting to note that there is a distinct thickening, in all ceratopsids, on or near the posterior rim of the external narial opening, in the region of the maxillary-premaxillary suture. In some modern planoarcuate skulls, there is a "maxillary tuberosity" in approximately the same position, above the anterior edge of the cheek tooth row, although it is entirely within the maxillary and, since the external narial opening is more anteriorly placed, it does not participate in the rim of this opening. In modern planoarcuate skulls, this tuberosity or node resists local stress concentrations (Tucker 1954) and possibly, the thickening in ceratopsids had the same function, resisting stresses from the nasal horn core and the anterior part of the dental battery that were concentrated in the posterior rim of the external narial opening. If this thickening acted to resist stresses, however, this was not its sole function. The medial surface of the narial region is poorly known in fossil reptiles (Parsons 1970) but it seems likely, from the enormous size of the external narial opening and the distance between the nasal bones, that the tissues of the nasal passages occupied a large area in ceratopsids and probably were very complex as well. In UA 11735 (Centrosaurus sp.) there is a distinct ridge, on the medial surface of the nasal, prefrontal and frontal, that runs postero-dorsally from the premaxillary-maxillary thickening to the anterior edge of the frontal fossa and a second ridge, below and posterior to the first, running from the posterior edge of the antorbital fenestra to a point slightly behind the posterior edge of the first ridge. These two ridges are connected, posteriorly, by a short curving ridge. The medial surface of the bones between the two major ridges is deeply excavated, especially posteriorly and the bone is deeply excavated behind the second ridge as well. (The posterior edge of this second excavation is the medial edge of the anterior wall of the orbit.) This area of the skull seldom is prepared in ceratopsids, so it is not possible to tell how many genera possess similar features, but part of a ridge, extending postero-dorsally from the premaxillary-maxillary thickening, is visible in UA 40 (*Eoceratops canadensis*), so it is possible that such ridges are present in all ceratopsids. Possibly, these ridges, or part of these ridges, supported cartilaginous conchae, projecting into the *cavum nasi proprium* (see Parsons 1970). If this interpretation is correct, the premaxillary-maxillary thickening could have been involved in supporting tissues in the nasal passages, as well as resisting stresses in this region. As mentioned above, all ceratopsids have some form of thickening in this region and in some genera, such as *Centrosaurus*, this thickening may be drawn out into a projection, indicating that resisting stresses was not its only function, since a simple node would resist stresses as well, or better, than a relatively slim projection. These projections may have supported part of the nasal conchae or other soft or cartilaginous structures within the nasal passage. In this case, the premaxillary-maxillary thickening could have functioned in a similar manner in all ceratopsids. Perhaps the ridges also transmitted stresses from the region of the brow horn core to the premaxillary-maxillary thickening.

Between the two dorsal ridges described for UA 11735 (*Centrosaurus* sp.), the medial surface of the skull roof forms a smooth curve interrupted only by a ventrally-projecting flange on the mid-line, anterior to the frontal fossa. This flange probably represents the true nasal septum (the rest of the septum being cartilaginous). The bony septum dividing the external narial opening, which is developed to some degree in all ceratopsids, should not be termed the "nasal septum", since this term refers to the solid, anterior prolongation of the braincase that separates the two nasal capsules (Romer 1956). The other septum, dividing the external narial opening of ceratopsids, is highly variable in extent and complexity and Sternberg (1949) suggested that this septum has taxonomic importance. According to Sternberg (1949, p.41), in *Eoceratops*, *Chasmosaurus*, *Anchiceratops*, *Torosaurus* and *Triceratops*, the osseus septum is "pierced by a well-defined fenestra" while in *Centrosaurus*, *Brachyceratops* and *Styracosaurus*, there is no such fenestra. In fact, the "fenestra" of the first group is often a pit, as in *Eoceratops* and *Pentaceratops* (which also belongs to this group). This pit may represent a secondarily closed fenestra or the septum may never have been pierced at all, so perhaps this group should be described as having a complex, rather than a smooth osseous septum. Also, despite Sternberg's statement (1949), the osseous septum dividing the external narial opening of Torosaurus is largely or wholly restored in all three known skulls (Colbert and Bump 1947), so it is not possible to describe this area of this genus. Based on similarities in other regions of the skull, however, Sternberg's statement probably is correct, although it cannot be corroborated as yet. The pit in the osseous septum of Eoceratops and related genera strongly suggests the presence of a soft tissue structure, perhaps a gland, and possibly the fenestra in the septa of certain specimens served a similar function, although in some specimens it seems likely that this fenestration is due to damage to the delicate bone forming a pit, rather than being a true fenestration. The septum itself, even without reference to the fenestra or pit, is highly variable in extent and complexity. In Centrosaurus and Styracosaurus, the septum is a large, smooth crescent, lacking projections or thickenings except at the base, where a low ridge supports the septum on each side. In both Centrosaurus and Styracosaurus there is a large projection at the premaxillary-maxillary thickening, a development found elsewhere within the Ceratopsidae only in Monoclonius and Pachyrhinosaurus, which is closely related to Centrosaurus and Styracosaurus. Brachyceratops has a similar osseous septum - large, smooth and cresent-shaped - but it lacks the ventral ridges bracing the septum and the projection at the premaxillary-maxillary thickening is relatively small. All of the genera with either a pit or a fenestra in the septum have a strong, vertical ridge posterior to this feature, presumably to compensate for the loss in strength caused by thinning or perforating that portion of the septum; and all of these genera, except *Triceratops* and *Anchiceratops*, have triangular projections on the postero-ventral edge of the septum, projecting into the external narial opening. While no such projection is found in *Anchiceratops*, the posterior edge of the septum being smooth, in *Triceratops* there may be a low flange in approximately this position. Whether this flange or projection supported some soft tissue structure or developed in respose to particular stresses in the narial region, or both, is uncertain. Although the osseous septum of ROM 5135 (*Arrhinoceratops brachyops*) is so badly preserved that Parks (1925) did not attempt to restore it, enough bone remains to indicate that *Arrhinoceratops* can be grouped with *Triceratops*, *Pentaceratops*, *Eoceratops* and *Chasmosaurus*. The septum of *Arrhinoceratops* appears to have been pitted but not fenestrated, with a short posterior flange, as in *Triceratops flabellatus*.

Whatever other functions this osseous septum had in the way of supporting soft tissue structures, it certainly must have affected the distribution of stresses in the anterior narial region and since the shape of the septum is correlated with the size of the nasal horn core, it is possible that its stress-related function was of paramount importance. In *Styracosaurus*, *Centrosaurus* and *Brachyceratops*, where the septum is large and smooth, the nasal horn core is much larger than the brow horn core, whereas in the other genera, the nasal horn core tends to be smaller than the brow horn core. (It is interesting to note that in ROM 5436 (*Chasmosaurus brevirostris*), where the nasal horn core is much larger than the brow horn core, the osseous septum is relatively large and crescent-shaped, as in *Styracosaurus* and *Centrosaurus*, and the posterior projections are relatively small. In *Brachyceratops*, on the other hand, where the nasal horn core is large but relatively smaller than in *Styracosaurus* and *Centrosaurus*, the septum is relatively smaller as well, and lacks the postero-lateral supporting ridges seen in those genera.) From these observations, it seems likely that the osseous septum in species with large nasal horn cores served primarily in resisting the stresses generated by the use of the horn core. In species with more complex septa, these septa functioned both to resist stresses transmitted from the nasal horn core and to support soft tissue structures that possibly were not found in other genera.

Thus, stresses from the weight and use of the nasal and brow horn cores appear to have been as important as the masticatory stresses in shaping the ceratopsid skull. The brow horn core affected such characters as the frontal fossa and secondary roofing over the braincase, the early coössification of dorsal mid-line sutures, thickening of the dorsal antorbital area and of the orbital rim (and probably the incorporation of palpebral ossifications into the antero-dorsal orbital rim as well), thickening of the angular region of the squamosal and, possibly, the development of ridges on the medial walls of the narial region, while the nasal horn core affected the early fusion of more anterior dorsal mid-line sutures, the form and extent of the osseous septum and probably the formation of the premaxillary-maxillary thickening. (Note that Brown and Schlaikjer (1940*b*) also felt that the posterior rim of the external narial opening functioned in transmitting stresses from the nasal horn core.)

The effects of stresses generated in the occiput from supporting the massive head have been discussed already. Most of the muscle attachments on the occiput probably were fleshy, judging by the smooth scars they left, and these muscles would have produced dispersed stresses that were resisted locally. The conspicuous exception to this generalization is the *ligamentum nuchae*, which produced a strong median ridge in much the same way as the Bodenaponeurosis influenced the development of the coronoid process. Undoubtedly the *M. spinalis capitis* and the *ligamentum nuchae* supported most of the weight of the head and large stresses would have been developed in the area of their attachment to the occiput. These stresses appear to have been resisted locally, though, for there is no evidence of structures for the transmission of these stresses to other areas of the skull, unless some were transmitted to the frill and lower jaw (via the stout quadrates) by the exoccipitals. The exoccipitals of ceratopsids are large, flaring distally at their contacts with the squamosals (see Fig. 22). The exoccipitals brace the posterior edges of the quadrates and the anterior part of the squamosals, and probably their major function was to assist in supporting the frill, especially anteriorly, where the bones of the frill are thick and heavy, and to help lock the proximal ends of the quadrates into position. The entire exoccipital is very stout, however, and it may have had some function in transmitting stress from the occiput as well.

(e) Structure and function of the frill

Of all the features of the ceratopsian skull, probably the frill, with its variable size, shape, ornamentation and fenestration has provoked the most discussion and controversy, both with respect to the identity of the elements forming the frill and the functions of the various parts of the frill. Although protoceratopsids such as Bagaceratops and Microceratops and the psittacosaurs do not possess a frill, these forms do have a sharp, elongated area of the parietal that gave rise to the large, ornate frills of the later ceratopsians so that the frill (or its precursor, in psittacosaurids and some protoceratopsids) is one of the most distinctive features of the whole sub-order Ceratopsia.

Because it is such a conspicuous feature and because its development has so modified the rest of the ceratopsian skull, the function of the frill has been debated widely. Many authors, including Lull (1908, 1933), Haas (1955), Ostrom (1964*a*, 1966) and L. S. Russell (1935) have stated that the frill functioned largely, if not entirely, as a platform for the origin of the major jaw adductor muscles but as shown above, such a function would have been possible only in *Leptoceratops*, *Microceratops*, *Bagaceratops* and the psittacosaurs. In *Protoceratops* and all the ceratopsids, the frill must have had other functions, for the *M. adductor mandibulae externus* did not extend posterior to the supratemporal fenestra, so that only the very anterior part of the frill could have served for muscular attachments. Other authors, although generally accepting the theory of muscle attachment to the dorsal surface of the frill, have proposed additional functions for the frill. Farlow and Dodson (1975) pointed out that the elaborate and various ornamentation of ceratopsian frills hardly can be explained by muscle attachment and jaw mechanics. By analogy to modern horned tetrapods, both mammalian and reptilian, Farlow and Dodson (1975, p.355) suggested that "the display function of the ceratopsian frill was probably at least as important as jaw mechanics in determining its morphology." Certainly, given that most ceratopsians possessed a large, conspicuous frill, usually embellished with various spikes or processes, it seems unlikely that the frill did not have at least some function in display, species recognition or other aspects of behaviour. Since there is considerable sexual dimorphism in *Protoceratops* (Kurzanov 1972), functions connected with behaviour may have modified the basic structure of the frill to some degree but it seems inconceivable that the development of such large masses of bone, producing profound changes in the rest of the skull and the anterior part of the post-cranial skeleton, should have been controlled to any large degree by display functions. Farlow and Dodson themselves mention that the crests of chameleons are formed largely of skin and other soft tissues and since they postulate head-to-head combat in ceratopsians using the horns, not the frill, it is unclear why a similar, light-weight crest would not serve the needs of display as well as a heavy osseous one, considering that the area of muscle attachment probably was restricted to the anterior regions of the frill. Kurzanov (1972) proposed that adult *Protoceratops* males had larger frills than females or juveniles and that these frills were used to attract mates and to frighten off rival males. Although one cannot be sure, from cranial evidence alone, that skulls with large frills do indeed belong to males and further, that protoceratopsid social behaviour was similar to that of modern "frilled" lizards, it is possible that *Protoceratops*, and perhaps other ceratopsians as well, did behave in the manner suggested by Kurzanov. The fact that in many modern lizards such display structures are erectile, however, being formed of soft tissues, plus the fact that ceratopsian frills are relatively far larger and heavier proportionally than the rudimentary frills of modern lizards, suggests that display alone cannot account for the development of any part of the ceratopsian frill except superficial variation in size and ornamentation.

Tait and Brown (1928) proposed that the frill protected the segment of the spinal cord passing between the foramen magnum and the neural canal of the fused anterior cervical vertebrae, which otherwise would have been exposed except for soft tissue. Again, while the crest certainly did perform this function, it is unlikely that such an elaborate and extensive frill developed solely or even largely for this purpose. Several other authors have postulated that the ceratopsian frill was a defensive structure. Colbert (1961, p.169) believed that the frill functioned "as a sort of buckler to protect the neck and shoulders, always a vulnerable region" and Lull (Hatcher, Marsh and Lull 1907, p.195) noted that "the development of the frill in the Ceratopsia has been considered as meeting the necessity for a better protection of the neck blood vessels from the weasel-like attack of small but bloodthirsty quadrupeds"! While the anterodorsal and anterolateral portions of ceratopsid frills are thick enough to be an effective defense, most of the rest of the frill is too delicate, even in Triceratops, where the frill is not fenestrated, to be an adequate defense against large carnivores or other ceratopsids. In Chasmosaurus, Pentaceratops and probably in Eoceratops, the frill is a large open frame that would stop a violent attack only at its edges. In other genera with fenestrated frills, the bone around the fenestrae is extremely thin, as it is in the center of the fused parietals of Triceratops, and could not have stopped any attacker large enough to pose a threat to a ceratopsian, and the fenestrae themselves, being covered by soft tissues, would not be an effective shield either. In this respect, the theories of Kurzanov and Farlow and Dodson seem more realistic in explaining the defensive function, if any, of the ceratopsian frill. Further, as Lull (1903) has pointed out, in some species, such as Triceratops serratus, the squamosal-parietal suture is a simple butt joint for much of its length and could not have withstood any bending, shearing or tensional stresses, which indicates further that the frill was not used to fend off violent attack. Lull (1905, p.421) felt that in some species, such as Triceratops hatcheri, the frill was "of greater protective value" than in others but in no ceratopsid is the whole frill thick enough to form an effective defense.

Klaauw (1952) considered enlargement of the origin of the "M. temporalis" to be the main function of the ceratopsian frill but he also believed that it had a defensive role and "some importance in connection with the position of the center of gravity of the whole body" (Klaauw 1952, p.498), although he did not elaborate on this last idea. In ceratopsids the dental battery is longer and heavier, incorporating more teeth, and the antorbital region of the skull is relatively much larger than in protoceratopsids, so it is quite probable that part of the development of a heavy, elongate frill was due to the need for counterbalancing the heavy anterior portion of the skull. Even in *Protoceratops*, the frill becomes larger with age as the number of teeth increases and the whole anterior region of the skull becomes larger and heavier. Significantly, in relatively long-faced ceratopsid species and/or species with relatively large horn cores, the frill usually is either very long, as in *Pentaceratops*, very thick, as in *Anchiceratops ornatus*, or covered with large spikes and processes, which are largest posteriorly to give the best leverage in the use of the head, as in *Centrosaurus* and *Styracosaurus*. (Such "balancing" devices need not provide a perfect equilibrium, as the *ligamentum nuchae* and muscles attaching to the occiput would help balance and control the heavy head.) Correspondingly, in *Arrhinoceratops brachyops*, which has a relatively short face and a short nasal horn core, the frill is only moderately long, lacking the large heavy processes seen in many other species, and the whole frill, except for the central parietal bar, is very thin (Lull 1933). In this species, as in *Triceratops*, the large brow horn cores are almost in line with the center of gravity of the skull and the anterior part of the face is relatively short, so a shorter, lighter frill would suffice to balance the skull.

Part of the function of the anterior region of the frill was to provide an area of attachment for the neck muscles but these muscles occupied relatively the same area in all species, never migrating beyond the anterior rim of the parietal fenestrae (or equivalent region, in *Triceratops*). The need to retain a certain freedom of movement of the head would prevent further migration of these muscles so that after a certain increase in the weight of the anterior region of the skull it would be necessary to increase the weight of the frill, rather than increasing the mass of the cervical musculature, to prevent the skull from becoming excessively heavy anteriorly. This theory requires only that the frill be lengthened and/or elaborated with heavy processes; it does not dictate the precise form of such processes nor the exact shape of the frill, both of which probably were influenced by behavioural characteristics such as display.

Brown (1914*a*, p.541) suggested that the epoccipitals of *Anchiceratops* "probably served the same purpose as similar structures in the living *Phrynosoma*" but when Whitford and Whitford (1973) reported the use of head spines as a defensive weapons in *Phrynosoma cornutum*, the encounter involved one lizard climbing on the back of another, which defended itself by jabbing up and back with its spines.

While such a defense might have been useful in repelling large carnivores, by analogy with modern mammals with large horns and with horned chameleons (Bustard 1958; Gans 1967), ceratopsians probably endeavoured to discourage enemies by frontal display and assault. Further, although horny sheaths applied to the surface of the epoccipitals might have been sharp in some or all ceratopsids, only in *Styracosaurus* are the epoccipitals themselves fairly sharp, suggesting that ceratopsids such as *Anchiceratops*, with blunt epoccipitals, may not have had weapons suitable for such an assault as *Phrynosoma* uses. Brown's theory also does not explain the function of the smaller epoccipitals and undulations characteristic of many ceratopsid species, which seem more likely to be display characters than weapons for active defense.

In constructing a lever to counterbalance the weight of an object, it is most efficient to place another weight at the end of the lever, at some distance from the fulcrum, since placing the balancing weight at a distance from the fulcrum produces the same force as would a greater weight closer to the fulcrum. In applying this principle to the ceratopsian frill, the occipital condyle-atlantal articulation is the fulcrum, the anterior part of the skull is the weight that must be balanced (a certain part of this weight will be balanced by the neck muscles, but these are ignored here for the sake of simplicity) and the frill is both lever and balancing weight. Thus, it is not surprising that in *Styracosaurus*, *Centrosaurus* and *Anchiceratops* there is a concentration of bony processes at the rear of the frill while in *Pentaceratops*, *Chasmosaurus*, *Protoceratops*, *Arrhinoceratops* and probably *Brachyceratops* and *Eoceratops*, there is a bony bar, of variable thickness and width, posterior to the frill fenestrae. In *Triceratops* also, the posterior part of the frill is thicker than the bone on either side of the median parietal bar, which is extremely thin. In all these genera, the squamosals and the central part of the parietal provide a bony framework of sufficient strength to support the length and weight of the frill. According to Badoux (1966, p.242): "the basis of the perfect frame[1] is the triangle, which has three members and three joints. For every additional joint two more bars will be required in building up a more complex frame, which is always divisble into triangles." Thus, the ceratopsian frill can be analysed as a perfect frame with three members, formed by the posterior parietal bar and the two squamosals, and this frame can be divided into two smaller perfect frames, one on each side, with the three members formed by the median parietal bar, the squamosal and one half of the posterior parietal bar. The frills that correspond most nearly to this description are the frills that are relatively very long (*Pentaceratops* and *Chasmosaurus*), while moderately long frills correspond only partly to this description and the short (with respect to the main body of the frill) frills of Centrosaurus and Styracosaurus do not fit this pattern at all. In genera with long frills, the frill would have been subjected to large bending forces by virtue of its long lever arm (the length of the frill), and the framed structure would help resist such forces. In shorter-frilled genera, such forces would be reduced, although in cases such as Styracosaurus, with heavy posterior ossifications, the frill has been reinforced by thickening the members. In these forms, the frame usually is redundant (having more members than needed to form a perfect frame (Badoux 1966)), rather than perfect. All bones represent a compromise of solutions to many different structural and functional problems (Fox 1964), however, so one method of analysis can never account for all the features of a particular bone and the theory of framed structures accounts for the shape of the frill better in some genera than in others.

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[1] "A perfect frame is one which has just sufficient members to keep it stable in equilibrium under any system of external forces acting at its joints without change of shape" (Badoux 1966, p.241).

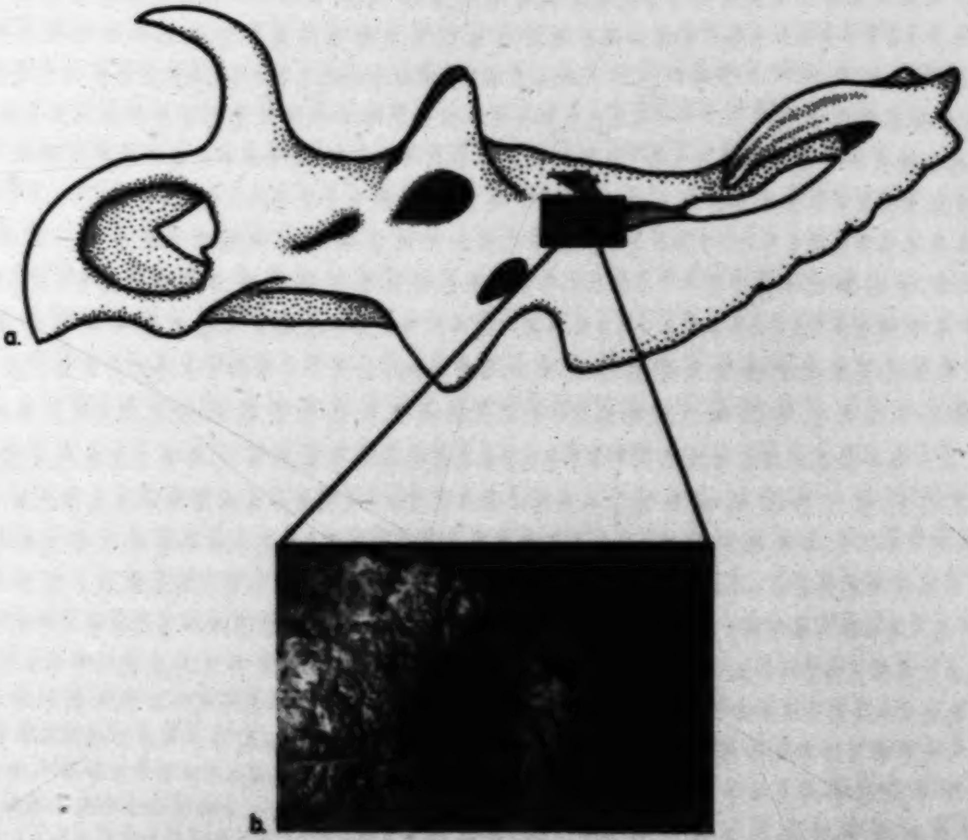
The areas of the ceratopsid frill that do not form members of a frame, either perfect or redundant, are thinned or fenestrated because the bone in these areas does not contribute to the structural strength or the function of the frill and presumably, there is a metabolic advantage in not producing or maintaining unneccesary bone. Several authors have suggested that the main frill fenestrae gave an increased area of attachment for the jaw adductors and/or allowed these muscles to bulge freely upon contraction but if the musculature did not extend as far back as the frill fenestrae, neither of these theories can be correct. Further, the thin rims of the fenestrae seem unlikely areas of attachment for large, powerful muscles and a fenestra to permit ventral bulging of the muscle would be unnecessary, considering that dorsally the muscle would be covered only by skin.

The fact that in some specimens the frill fenestrae are of vastly different sizes and/or the frill has fenestrations other than the usual ones in the parietal, tends to support the theory that the development of such fenestrae was due to a metabolic saving, rather than an active function. If the primary consideration was lightening the frill, bone would be thinned or lost in all unstressed areas (Fox 1964) and the precise shape and size of the fenestrae would be less important than the amount of bone lost. In Chasmosaurus and Pentaceratops, the central portion of the squamosals is thinned and in all ceratopsids, the parietal is thinned on either side of the median parietal bar. Presumably these areas were unstressed in life and could most easily be thinned without reducing the structural strength of the frill as a whole. Those specimens that have "extra" fenestrae also tend to have these features in relatively unstressed areas of the skull. ROM 5135 (Arrhinoceratops brachyops) has a single, large fenestra in the left squamosal, in the thinnest portion of that bone and Lull's

(1933) Specimen "A", in Upsala, Sweden (*Pentaceratops fenestratus*) and ROM 5436 (*Chasmosaurus brevirostris*) have similarly placed, unpaired fenestrae while USNM 2412 ("*Diceratops*" (=*Triceratops*) *hatcheri*) has a large fenestra in the left squamosal, a smaller one in the right squamosal and a very small one in the thin, right-hand posterior-central area of the parietal (see Hatcher 1905, pl. XIII). Although some authors have described these fenestrae as pathological, being either wounds or the result of disease, I believe that all the examples cited above are due to perforation, by resorption, of unstressed areas of the frill. Although the metabolic saving in the case of very small fenestrations would be negligible, it is possible that these fenestrae would have enlarged with time, had the individuals involved lived longer, or possibly, these perforations are pathological in the sense that they represent the abnormal amplification of some signal that provided for thinning of these areas. That they are not due to disease is evident by the fact that the edges and surrounding bone lack the rugose callosities and deformities commonly associated with bone lesions and tumours. Also, although Lull (1933) felt that the numerous "injuries" found in ceratopsian skulls proved that ceratopsians were "pugnacious", and though wounds and the results of disease are apparent in certain skulls, the fenestrae mentioned above cannot be due to mechanical injury for they do not show the characteristics of bone that has been punctured or damaged by impact. Gurdjian and Lissner (in a series of experiments reviewed by Evans (1957), from whom the following discussion was taken), showed that upon impact, bone bends inward, producing tensile strain in circular and radial directions around the site of impact. The circular tensile strain produces radially oriented cracks that lie relatively distant from the site of impact while the radial tensile strain produces concentrically oriented cracks closer to the site. Depending on the bones involved, only one of these sets of cracks may appear but in the case of the "extra" fenestra described above, neither set is visible, either as persistent or as rehealed fractures.

Various ceratopsid skulls do show pre-mortem damage and some of these wounds may have been caused by fighting with other ceratopsids but in all of these examples there is clear evidence of bone deformation, rather than the smooth surfaces surrounding the fenestrae described above. YPM 1828 (*Triceratops* ("*ingens*") *horridus*) has a large, rehealed fracture extending over much of the right side of the frill, with a thick callosity covering the area of fracture. Erickson (1966, p.3) described a "premortem puncture wound" in the jugal of SMVP P60/2/1 (*Triceratops prorsus*), and Lull (1933) described a puncture wound in YPM 1830 (*Torosaurus latus*), anterior to the right orbit, which appears to have been infected, as the bone surrounding and forming the floor and walls of the wound is rough and cancellous, as if damaged by disease as well as injury (Fig. 38c).

Fig. 38. a. Left lateral view of skull of UA 11735 (*Centrosaurus* sp.). (Area shown in b. covered by solid rectangle.) b. Detail of probable puncture wound on left squamosal of UA 11735. c. Possible puncture wound or tumour anterior to right orbit of YPM 1830 (*Torosaurus latus*).


a.
b.

c.

Alternatively, this wound may be due to a tumour, rather than a puncture. One wound that is very likely to be a puncture wound, possibly from another ceratopsian, occurs on the left squamosal of UA 11735 (Centrosaurus sp.) (Fig. 38a, b). Not only is there a roughened circular depression, the partially rehealed site of impact, but on the medial surface of the squamosal, opposite the depression on the lateral surface, there are concentric strain cracks surrounding a radial pattern of strain cracks, in precisely the pattern described by Evans (1957). Since the external surface of this wound is at least partially rehealed, judging by the thickness and rugosity of the bone compared to the equivalent area on the right side of the skull, it is likely that this injury occurred during life.

UA 40 (Eoceratops canadensis) has a rough, circular, flattened area on the anterodorsal surface of the left squamosal that probably is pathological, for it does not appear in the type specimen of Eoceratops canadensis (NMC 1254) and it is not near an area of muscle attachment. Since this scar is not very deep, it may have been caused by an infection of the skin covering this area. The region of the dorsal skull roof between the orbits of NMC 8800 (Chasmosaurus russelli) has been badly distorted by crushing but part of this distortion probably is pathological as well, since the area is highly rugose and contains several large perforations that Sternberg (1940) considered to be pathological. The skull of NMC 8790 (Monoclonius lowei) also shows pathological features since the right side of the parietal lacks a fenestra (although traces of a fenestra are present on the left side of the parietal) and Sternberg (1940) regarded this closure as the result of an injury to the frill.

In the earliest ceratopsians, then, the early protoceratopsids and the psittacosaurids, the precursor of the frill found in later protoceratopsids and the ceratopsids probably functioned entirely as an increased area for the attachment of the powerful adductor muscles associated with the strong shearing and crushing actions of the increasingly heavy jaw. As the anterior portion of the ceratopsian skull became increasingly specialized, with respect to dentition especially, but also with respect to the elongated nasal area, the brow horn cores, the orbits and so on, it became increasingly heavy and the frill became elongate, behind the region of muscle attachment, in order to counterbalance the rest of the skull. Fenestrations developed in this frill to lighten the unstressed areas where bone was not needed but in *Triceratops*, the main fenestrae closed secondarily, presumably in response to a secondary shortening of the skull and hence, of the frill. Other functions such as display, and possibly defense, modified the appearance of the frill still further, producing the array of shapes and ornamentation seen within the Ceratopsidae.

III. Phylogeny of the Ceratopsia

(a) Relationships of *Eoceratops*

When Lambe established the genus *Eoceratops* in 1915, he intended the name to imply an ancestral relationship to the genus *Triceratops* but since the two specimens here assigned to *Eoceratops* have been included at various times in *Ceratops*, *Monoclonius* and *Chasmosaurus*, one cannot merely accept Lambe's authority in aligning *Eoceratops* with *Triceratops*.

As shown above, *Ceratops* is a wholly indeterminate genus, the type material being insufficient to sustain meaningful comparisons with other specimens. Lambe (1915) considered *Monoclonius* to be indeterminate as well but while there seems to be a concensus concerning the indeterminate status of the genus *Ceratops*, there has been considerable controversy surrounding the genus *Monoclonius*. Sternberg (1938, 1940) discussed the relationships of *Monclonius* and concluded that while this genus is closely related to *Centrosaurus*, the two are not identical and both are valid, distinct genera, although of the numerous species referred to *Monoclonius*, only *M. crassus* (the type species), *M. sphenoceras* and *M. lowei* can be assigned without question to *Monoclonius*. Sternberg based his argument on the difference between the posterior parietal bar in the two genera, that of *Monoclonius* being broad and thin with only a slight posterior excavation and a thin undulating edge whereas that of Centrosaurus is thickened and supports heavy epoccipitals, large anterior and posterior processes and a strong posterior excavation (Sternberg 1938). (Sternberg (1938, 1940) also distinguished between the two genera on the basis of differences in the nasal region.) In this work, only specimens referable to Centrosaurus, by Sternberg's definition the largest and best known genus, were examined but since Monoclonius and Centrosaurus are similar in most respects, most references made to Centrosaurus extend to Monoclonius as well.

Eoceratops cannot be closely related to either Centrosaurus or Monoclonius as the frill and the narial region are entirely different. In Centrosaurus (and Monoclonius) the frill is short and broad with a widely flaring squamosal and a broad rectangular parietal. The median parietal bar in Centrosaurus is relatively very broad and the parietal fenestrae are round and relatively small. Although much of the frill of Eoceratops is unknown, the preserved parts are utterly unlike comparable regions of the Centrosaurus frill. The squamosal is flat and triangular, closely appressed to the anterior extension of the parietal and not flaring laterally as in Centrosaurus, and the anterior extension of the parietal is thin and triangular, not broad and flat as in Centrosaurus. The median parietal bar is relatively thin and appears to have bounded fenestrae that were closer to those of Chasmosaurus than Centrosaurus, the whole parietal probably being more triangular than rectangular and the frill long and relatively narrow, rather than short and broad. The narial regions of *Centrosaurus* and *Eoceratops* also are very different, in respect to the characteristics of the premaxillary septum, the ventral edge of the premaxillary, the premaxillary-maxillary tuberosity and the posteroventral projection of the premaxillary that articulates with the ventral portion of the nasal. Correlated with the differing ventral premaxillary borders, the dorsal edges of the predentaries of *Centrosaurus* and *Eoceratops* differ as well.

Lull (1933) assigned UA 40 (now *Eoceratops*) to *Chasmosaurus* and the original field identification of the specimen was *Chasmosaurus* as well. Certainly this assignment is closer than the assignment to *Monoclonius* but there are sufficient differences to distinguish *Eoceratops* from *Chasmosaurus*. *Eoceratops* is characterized by a short squamosal, although the relative proportions of the frill probably were similar to those of *Chasmosaurus*; the face of *Eoceratops* is relatively short; the brow horn cores are long; and the lateral temporal fenestra is small and placed very high up on the side of the skull. This combination of characters is not found in any specimen of *Chasmosaurus* and cannot be dismissed as mere ontogenetic variation for UA 40 is a fully adult individual. It is possible that Lull (1933) was correct and UA 40 (and possibly NMC 1254 as well) could be a sexual variant of *Chasmosaurus*, but not enough specimens are known to make such a statement at the present time. In the absence of large numbers of specimens, there are as many structural features distinguishing *Eoceratops* from *Chasmosaurus* as, say, distinguish *Chasmosaurus* from *Pentaceratops*, so that *Eoceratops* appears to be a valid genus rather than a variant of *Chasmosaurus*. (Sternberg (1927*b*) also considered *Eoceratops* and *Chasmosaurus* to be distinct genera.)

Whereas *Eoceratops* is closely related to *Chasmosaurus*, and relatively distant from *Monoclonius*, its relationships to *Triceratops* are more obscure. *Triceratops* itself often has been aligned with *Monoclonius*. Lull (1933) felt that either *Monoclonius* or *Arrhinoceratops* may have produced the *Triceratops* lineage, Hatcher, Marsh and Lull (1907) included *Monoclonius* and *Triceratops* in a single lineage, and Colbert (1948, 1961) and Ostrom (1966) also derived *Triceratops* from *Monoclonius*. One of the main reasons for including *Triceratops* and *Monoclonius* in the same lineage has been the length of the frill. Several authors (*e.g.*, Ostrom 1966) have divided the Ceratopsidae into "long-frilled" and "short-frilled" genera. According to Ostrom's definition (1966, p.296), in "short-frilled" genera, "the postfrontal length of the frill is less than or approximately equal to the basal skull length", while in "long-frilled" genera, "the postfrontal length is much greater than the basal skull length." Further, "all short frills are broad and rounded in posterior outline", while "all long frills are rectangular rather than rounded in outline" (Ostrom 1966, p.296). By these criteria, *Triceratops* does seem closer to *Monoclonius*, *Centrosaurus*, *Styracosaurus* and *Brachyceratops* than to other ceratopsids but analysis of the shape of the individual elements of the frill indicates that these similarities may be due to convergence rather than close relationship. The frill in *Triceratops* is short, as in *Centrosaurus*, but the shape and orientation of the squamosal are closer to the condition in long-frilled genera, with a triangular squamosal that reaches the posterior border of the frill, rather than flaring broadly, as in *Centrosaurus*. Further, the parietal is more nearly triangular than rectangular, as it is in *Centrosaurus*, and the round outline of the posterior border is largely a function of the relatively short squamosals. Sternberg (1949) felt that the Ceratopsidae should be divided into long- and short-*squamosaled* genera, depending upon the distance of the squamosal from the posterior border of the frill. (This definition would include in the long-squamosaled group both genera in which the squamosal reached the posterior edge of the frill and those in which the parietal projected somewhat beyond the squamosal.) By this criterion, *Triceratops* is closer to *Chasmosaurus*, *Torosaurus*, *Arrhinoceratops*, *Pentaceratops* and *Anchiceratops* than to *Centrosaurus*, *Monoclonius* and *Styracosaurus*. Sternberg (1949) also stated that the premaxillary septum is fenestrated in the long-squamosaled forms. Some long-squamosaled species lack such fenestrae but these forms invariably possess a pit in the same region, a feature that does not appear in the short-squamosaled genera (see above) and by this criterion as well, Triceratops belongs with the long-squamosaled forms. Further, Triceratops is characterized by long brow horn cores and a short nasal horn core and while this pattern is not present in some long-squamosaled genera, it is present in none of the short-squamosaled genera, all of which have relatively very large nasal horn cores (or a nasal boss, in the case of Pachyrhinosaurus) and extremely short brow horn cores. Thus, it is likely that the similarites between Monoclonius and Triceratops are due to convergence, Triceratops being derived from a long-squamosaled lineage that tended to secondary reduction of the length of the frill and closure of the frill fenestrae.

Lambe (1915) distinguished three lineages of ceratopsids: Eoceratops-Triceratops, Centrosaurus-Styracosaurus-Brachyceratops, and Chasmosaurus-Torosaurus but his separation of the Eoceratops-Triceratops lineage from the Chasmosaurus-Torosaurus lineage was based on the relatively shorter frills of the former, a distinction not made in the present work, where the shorter-frilled genera Eoceratops, Arrhinoceratops and Triceratops are regarded as offshoots of the Chasmosaurus lineage. (Certainly Eoceratops cannot be placed in a separate lineage from Chasmosaurus, since these two genera are extremely similar.) There are several similarities between *Triceratops* and *Eoceratops*, such as the reduction in the relative length of the frill, the relative proportions of the brow and nasal horn cores, and the relatively short facial region, although some species of *Triceratops* vary with respect to this last character. *Eoceratops* appears to have had relatively large parietal fenestrae, however, probably similar to those of *Chasmosaurus*, while in *Triceratops* the main parietal fenestrae are closed, although the extremely thin lateral parts of the parietal indicate that *Triceratops* is derived from a ceratopsid with parietal fenestrae. *Arrhinoceratops* is closer to *Triceratops* in the size of the frill fenestrae, which are relatively smaller than (the reconstructed size) in *Eoceratops*, although the frill of *Arrhinoceratops* is relatively longer than in *Triceratops*. Further, the nasal horn core of *Arrhinoceratops* is quite close to that of *Triceratops prorsus* and could easily have given rise to a horn core of the type seen in *T. obtusus*, *T. eurycephalus* and *T. hatcheri*. *Arrhinoceratops* is certainly not as close to *Eoceratops* as *Eoceratops* is to *Chasmosaurus*, or even *Pentaceratops*, but both *Eoceratops* and *Arrhinoceratops* probably belong to an offshoot of the *Chasmosaurus* lineage, *Eoceratops* being quite close, *Arrhinoceratops* relatively distant from the branching point, and this lineage also produced *Triceratops*.

(b) Trends in structure within the Ceratopsia

While there seem to be two distinct lineages of ceratopsids, as Ostrom (1966) and others have suggested, the interpretation presented here differs from that of Ostrom (1966) in that *Triceratops* is placed within the same lineage as *Chasmosaurus* and *Eoceratops*. The "short-squamosaled" genera *Monoclonius*, *Centrosaurus*, *Styracosaurus*, *Brachyceratops* and *Pachyrhinosaurus* are united not only by characters of the frill, but by details of the narial and facial regions and characters of the lower jaw, so they seem to form a natural lineage. These genera are characterized by short, broad, rounded frills that may have large posterior epoccipitals or modified epoccipitals. All have short faces and narial regions characterized by a smooth, crescent-shaped premaxillary septum and a premaxillary-maxillary tuberosity developed as a projection into the external narial opening. All have a large nasal horn core (or nasal boss) and small, triangular brow horn cores or a rugosity over the orbit instead of a horn core. Within this lineage, *Monoclonius* and *Centrosaurus* are very closely related, possibly even congeneric, and *Styracosaurus* is closely related to both these genera, although probably not directly descended from either. Both *Centrosaurus* and *Styracosaurus* have smooth channels, possibly for muscles not developed in other genera, connecting the supratemporal fenestrae and the frontal fossa; both have similar frill proportions and large, modified epoccipitals on the posterior border of the frill.

Brachyceratops is closely related to these three genera but has more primitive features than any of them and *Pachyrhinosaurus* is a descendant of this lineage, although it exhibits several unique derived characters not seen elsewhere among the Ceratopsia.

All other ceratopsid genera belong to the long-squamosaled lineage but within this group there are several sub-lineages. *Chasmosaurus*, *Pentaceratops* and *Torosaurus* form the main lineage with *Anchiceratops* being an offshoot, probably of a form close to *Chasmosaurus*. *Eoceratops*, *Arrhinoceratops* and *Triceratops* belong to a separate offshoot but *Eoceratops* is quite close to the main stock, being especially close to *Chasmosaurus*. Neither *Eoceratops* nor *Arrhinoceratops* appears to be a direct ancestor of *Triceratops* but both show some similarities to this genus.

SUMMARY

Eoceratops canadensis is a relatively small ceratopsid from the Judith River (Belly River) beds of Alberta. A relatively short but triangular squamosal, dorsally placed lateral temporal fenestra, short triangular nasal horn core and long tapering brow horn cores distinguish this species from the closely related species *Chasmosaurus brevirostris*, *C. kaiseni* and *C. belli*.

The major cranial muscles of ceratopsids, including *Eoceratops*, are reconstructed as follows:

M. adductor mandibulae externus superficialis - arose from the fascia covering the lateral temporal fenestra and from the borders of the lateral temporal fenestra and inserted on the dorso-lateral surface of the coronoid process.

M. adductor mandibulae externus medialis and *profundus* - arose from the floor and walls of the supratemporal fossa and from the fascia covering the fossa and inserted on the coronoid process *via* a strong Bodenaponeurosis.

M. levator anguli oris - formed a lateral cheek, attaching to the medial surface of the jugal-quadratojugal process and the strong lateral ridges on the dentary, maxillary and jugal.

M. pseudotemporalis - arose from the anterior surface of the laterosphenoid and inserted on the antero-medial slope of the coronoid process.

M. pterygo-mandibularis ventralis - probably was divided, at least distally, into long and short heads, both of which arose from the posterior surface of the pterygoid, the long head inserting on the lateral surface of the angular and the short head inserting on a ridge below the Meckelian fossa.

M. pterygo-mandibularis dorsalis - arose from the ectopterygoid and inserted on the retro-articular process.

M. adductor mandibulae posterior - arose from the anterior slope of the quadrate and inserted in the Meckelian fossa.

M. levator bulbi - arose from the anterior surface of the laterosphenoid and inserted on the dorsal edge of the lower eyelid.

M. intermandibularis - connected the ventral borders of the two lower jaw rami.

M. depressor mandibulae - arose from the anterior edge of the squamosal and inserted on the retro-articular process.

The ceratopsid occiput shows surfaces of attachment for the *Mm. transversalis cervicis* and *ilio-costalis cervicis*, on the ventral edge of the exoccipital; the *Mm. transversalis capitis* and *ilio-costalis capitis*, on the basioccipital; the *M. subvertebralis*, on the basioccipital: the *M. obliquus capitis magnus*, on the exoccipital; the *M. rectus capitis posterior*, on the exoccipital; the *M. spinalis capitis* and *ligamentum nuchae*, on the parietal; and a possible area of attachment for an undivided *M. sternocleidomastoideus*, on the parietal.

The ceratopsid dentition indicates a primarily vertical jaw action, accompanied by rapid replacement of individual teeth, probably reflecting a diet largely composed of resistant or even woody fibrous tissue. This pattern varies considerably from the patterns seen in protoceratopsids and psittacosaurids.

The jaw action of ceratopsids combined a "static-pressure" system (Olson 1961) with vertical shear, a combination not found among modern vertebrates.

Variations in the premaxillary, rostral, nasal and predentary, combined with differences in proportion of the brow and nasal horn cores and of the bones of the frill indicate that *Eoceratops* belongs to the long-squamosaled lineage of ceratopsids, while *Monoclonius*, *Centrosaurus*, *Brachyceratops* and *Pachyrhinosaurus* belong to a short-squamosaled lineage. *Triceratops* is a specialized member of the long-squamosaled lineage.

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